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Fishery Bulletin

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PRODUCTIVITY GAINS IN U.S. FISHERIES

FREDERICK W. BELL AND RICHARD K. KINOSHITA[1]

ABSTRACT

Changes in productivity or annual landings per fisherman help to determine the economic welfare of the fishing industry. Although a study of productivity gains in various U.S. fishing fleets over the last 20 yr showed variations between fisheries, many sectors of the fishing industry experienced substantial increases in labor productivity in recent years. Of the 17 fisheries studied, 11 exhibited positive trends in output (landings) per fisherman. A productivity index was constructed which indicated that, in the aggregate, fishing labor productivity increased by approximately 2.5% per year during the 1950-69 period, compared with 3% for the entire U.S. economy. Upon comparison of the fishing industry with those of meat and poultry, the fisheries' chief competitors, it was shown that labor productivity advances in the U.S. fishing industry were the lowest. A similar analysis for selected foreign fishing sectors revealed that the United States had fallen behind other countries with respect to productivity gains. A detailed quantitative study of three selected fisheries showed that increases in aggregate fishing pressure significantly reduced labor productivity; however, this force was more than offset by increases in fishing effort per worker and technological progress in many fisheries. The quantitative impact of environmental, technological, and regulatory factors was also identified.

The growth in productivity or annual landings per fisherman is an important determinant of the economic welfare for the U.S. fishing industry.[2] Small or negative productivity gains in a fishery are often associated with lagging profits, wages, and employment because U.S. fishermen must compete with foreign fishery imports and other protein substitutes where productivity is a main ingredient of competitive advantage. Moreover, rising productivity in the fishery sector has helped reduce inflationary tendencies that have been most prevalent in meat and fish products. Productivity gains, in the long run, raise standards of living or reduce the amount of time we must work to produce a pound of fish or a television set or an automobile.

Generally, gains in productivity are determined by the increasing efficiency of our vessels and gear; the education, training, experience, and morale of our fishermen; and, of course, the condition of the fishery stock and other environmental factors.

This article will survey the gains in productivity experienced by various U.S. fishing fleets over the last two decades. Comparisons will be made between gains in fishing productivity and those in competing sectors. We shall also explore some of the reasons behind the gains in productivity for selected fisheries.

LABOR PRODUCTIVITY TRENDS IN SELECTED U.S. FISHERIES

Before we discuss productivity trends in selected U.S. fisheries, it will be instructive to look at the statistical definition of labor productivity that will be employed in this article. Productivity or annual landings per fisherman is obtained by dividing aggregate landings (for a year) by the number of fishermen employed.[3]

[1] Economic Research Division, National Marine Fisheries Service, NOAA, Washington, D.C. 20235.

[2] Productivity is usually measured in terms of output per man-hour. These data are not available for the U.S. fishing industry; we must therefore rely on annual landings per fisherman as a rough measure.

[3] As economists define it, productivity is simply a ratio of physical output to physical input. Higher productivity means getting more output with the same effort or the same output with less effort. "Total-factor productivity" can be calculated by dividing output by a figure that represents all the resources used, including plant and equipment, labor, and land. Theoretically, this is the true mea-

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For any particular fishery, the accuracy of data on aggregate annual landings is fairly reliable. However, the number of fishermen reported by the National Marine Fisheries Service is not adjusted for the extent of utilization during the year. For example, the U.S. Bureau of Labor Statistics collects detailed data on hours worked for most industries in the economy. This makes it possible to compute productivity on the output per man-hour basis. No universally comparable data are available on the fishing industry. Hence, our statistical base is something less than perfect.[4] Systematic variations in days and hours worked per year may be a biasing factor, but it is hoped that they are random. In addition, the reader should note that we are comparing rates of growth in productivity among fisheries and other industries and not absolute differences in productivity.

Table 1 shows the compound annual growth rate of labor productivity for 17 of the nation's major fisheries over the 1950-69 period.[5] Notice that the Gulf of Mexico blue crab, Atlantic clam, and Gulf of Mexico menhaden fisheries all had rates of productivity advance over 5%. Unfortunately, some of our largest fisheries such as Gulf of Mexico shrimp, Atlantic sea scallop, Atlantic and Gulf of Mexico oysters, and Alaskan salmon exhibited negative trends in productivity.

One interesting aspect of the growth in labor productivity is its year-to-year fluctuation. This is important for a variety of reasons. Many fishermen are paid according to the "lay" agreement where fishermen and vessel owners share the value of the catch on some predetermined basis. Short-run oscillations in labor productivity may contribute to an unstable earnings pattern.[6] Other industries have fixed wage agreements that depend on secular rather than short-run changes in productivity. To get some idea of which fisheries are more subject to oscillations in labor productivity, we constructed an index of instability which measures the percentage fluctuations around the long-run time trend in annual landings per fisherman.[7] Table 2 shows the 17 fisheries discussed earlier ranked according to cyclical instability in labor productivity. Using the most unstable as a base (i.e., Gulf of Mexico blue crab pot fishery), we see that 13 of the fisheries have less than one-half the instability of the base fishery.

Although the performance of individual fish-

TABLE 1.—Ranking of fisheries by the rate of growth in output per fisherman, 1950-69.

	Fishery	Rate of growth[1]
1.	Gulf of Mexico blue crab pot fishery	[2]+7.8
2.	North-Middle Atlantic and Chesapeake Bay dredge clam fishery	[2]+7.0
3.	Gulf of Mexico menhaden	[2]+6.8
4.	Pacific yellowfin-skipjack tuna	[2]+4.5
5.	Pacific halibut	[2]+3.8
6.	North Pacific groundfish	[2]+3.1
7.	Atlantic menhaden	[2]+2.4
8.	Atlantic blue crab pot fishery	[2]+1.3
9.	Pacific albacore	+0.8
10.	Atlantic shrimp	+0.7
11.	North Atlantic groundfish	+0.5
12.	Pacific (excluding Alaska) Dungeness crab	−0.4
13.	Inshore American lobster	−0.5
14.	Gulf of Mexico shrimp	[2]−1.3
15.	Atlantic sea scallop (subarea 5Z)	−1.5
16.	Atlantic and Gulf of Mexico oyster	[2]−2.0
17.	Alaska salmon	[2]−3.1

[1] Linear least squares trends of the logarithms of output per fisherman.
[2] Trend was statistically significant at the 5% level.

sure of efficiency, but statisticians have trouble constructing the index number that serves as the divisor. They have to combine unlike quantities—hours of work and units of capital investment—into a single index. And while statisticians never hesitate to add apples to oranges, the results are questionable. Economists, therefore, usually work with a simpler concept, "partial productivity." This is the ratio of physical output to a single input, usually labor. In most discussions, "productivity" means "labor productivity" or real output per hour, day, or year of work. It is a rough measure of the effectiveness with which we use our most important productive resource-labor.

[4] See Appendix to this article on employment figures in the U.S. fishing industry.

[5] The growth rate in labor productivity was computed by fitting a logarithmic function, i.e. fitting a linear time trend to the logarithm of output per fishermen. The 17 fisheries represent 68, 71, and 58% by landings, value, and employment, respectively, for the United States.

[6] Generally, a contraction in landings—due to a decline in productivity—will reduce income per fisherman if prices do not change appreciably. Prices may not increase if foreign imports are significant and/or price elasticity is large (i.e., a large percentage drop in landings results in a small percentage increase in price).

[7] The formula used to construct the index was:

$$CV_y = \frac{\sum_{i=1}^{N} \left| 1 - \frac{Y_{c_i}}{Y_{o_i}} \right|}{N}$$

where CV_y = cyclical variation in labor productivity; Y_O = observed labor productivity; Y_C = computed labor productivity from the time trend; and N = number of years.

eries is important, we do want some summary measure to tell us how the entire fishery sector is doing with respect to the rate of growth in labor productivity. If so, we can compare this summary measure with other important sectors in the U.S. economy. Fortunately, we can construct an aggregate index of labor productivity. The construction of this index is rather technical in nature and will not be discussed in detail here.[8] Suffice it to say we cannot add the total pounds of fish landed in the United States and divide by the number of fishermen employed when constructing an aggregate index over a period of time. This is true since there may be appreciable shifts in the production of various species with differing absolute productivity, thereby biasing the index. (Therefore, the constructed index controls product mix.)

Constructing an index based on the 17 fisheries shown in Table 1, we find that aggregate productivity grew at an annual rate of 0.7%. To obtain a more representative figure for all fisheries, we added an 18th fishery, which represents the group of remaining U.S. fisheries not included in the original 17. The aggregate index showed productivity growth at an annual rate of 2.5% over the 1950-69 period.[9] However, there seems to be a noticeable tendency for the growth rate of fishermen's productivity to decline over the observed period; i.e., the annual growth rate over 1950-59 was 4.7%, but it slackened to 0.5% in the last 10 yr. This was probably a result of increasing fishing pressure in established fisheries (see section below on factors behind productivity advances). This index is plotted in Figure 1. On the average, the American fisherman has been able to raise his productivity significantly over the last 19 yr. This is especially encouraging when we realize that the fishermen, as opposed to their counterparts in manu-

TABLE 2.—Ranking of fisheries by the cyclical variation in output per fisherman, 1950-69.

	Fishery	Cyclical variation in labor productivity	Percent of largest
1.	Gulf of Mexico blue crab pot fishery	0.448	100.0
2.	Atlantic sea scallop (subarea 5Z)	0.298	66.5
3.	Pacific (excluding Alaska) Dungeness crab	0.242	54.0
4.	Pacific albacore	0.234	52.2
5.	Gulf of Mexico menhaden	0.204	45.5
6.	Atlantic shrimp	0.188	42.0
7.	Atlantic menhaden	0.157	35.0
8.	North-Middle Atlantic and Chesapeake Bay dredge clam fishery	0.148	33.0
9.	Alaska salmon	0.147	32.8
10.	Atlantic blue crab pot fishery	0.104	23.2
11.	Pacific yellowfin-skipjack tuna	0.104	23.2
12.	North Pacific groundfish	0.100	22.3
13.	Gulf of Mexico shrimp	0.095	21.2
14.	Pacific halibut	0.093	20.8
15.	North Atlantic groundfish	0.082	18.3
16.	Atlantic and Gulf of Mexico oyster	0.081	18.1
17.	Inshore American lobster	0.055	12.3

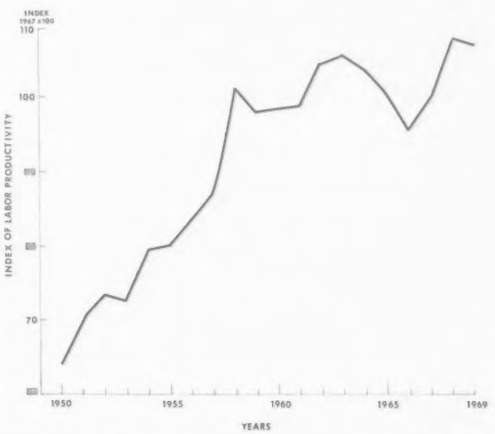

FIGURE 1.—Index of labor productivity for the fishing sector, 1950-69. (Productivity index is based on 17 individual fisheries and 18th residual category.)

[8] See "Output per man-hour measures: industries," (Bureau of Labor Statistics, 1966). Because of the problems with our data, it should be said that it was implicitly assumed that the work year is approximately the same for each fishery; a biasing factor may be introduced in the index to account for errors as a result of this assumption. However, as long as the difference in work years remains constant from fishery to fishery, this factor should not appreciably influence the time trend in the productivity index.

[9] The 18th fishery contained all residual fisheries or mostly minor fisheries that were too numerous to analyze separately. However, the rate of growth of labor productivity of the residual was fairly high. The reasons behind this finding are numerous. First, some of the residual fisheries are latent or newly developing, resulting in high productivity. Second, some duplication of fishermen operating in a number of fisheries is implicit in some of the data. That is, fishermen included in the 17 individual fisheries should also be counted in the residual. However, they were not since we merely subtracted the total number of fishermen in the 17 fisheries from aggregate employment (i.e., with no duplication). This would bias labor productivity in the 18th fishery upward. The reader should be aware of this technical problem that could not be solved with existing information.

facturing and service industries, must exploit a resource which has a fixed biological maximum that has a tendency to depress labor productivity (see discussion below).

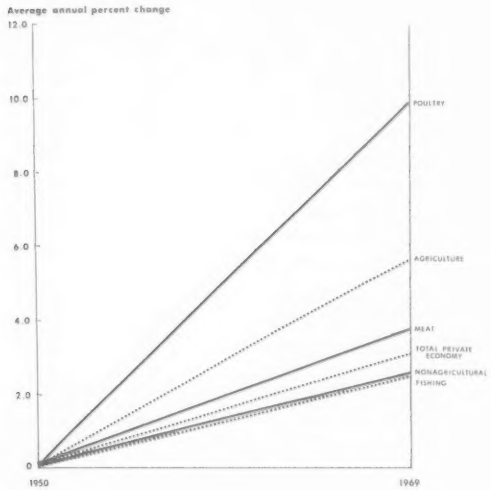

FIGURE 2.—A comparison of the rates of growth in labor productivity for the total private economy, agriculture, meat, poultry, nonagricultural, and fishing industries, 1950-69. (Source: U.S. Department of Labor, Bureau of Labor Statistics; U.S. Department of Agriculture, "Agricultural Statistics"; and Economic Research Division.

COMPARISON OF PRODUCTIVITY IN FISHING WITH OTHER SECTORS OF THE ECONOMY

Figure 2 shows a comparison of the growth in labor productivity over the 1950-69 period in the total economy, and specific categories encompassing all agriculture, meat, poultry, nonagriculture, and fishing industries.[10] The rate of growth in fishing was less than that for the U.S. economy as a whole. However, the rate of growth of labor productivity in agriculture was nearly twice that of the entire economy. Of special significance, changes in productivity in fishing lagged considerably behind that in the poultry industry and over one percentage point (per annum) in the meat industry. Since labor productivity is a prime ingredient in relative price changes, it may be concluded that these trends were generally adverse to the fishing industry.[11] That is, the more rapid advance in agriculture (including meat and poultry) lowered the price ratio of agricultural to fishery products. For example, the annual rate of growth (1950-69) in the wholesale price index of processed finfish was 3.9% while the wholesale price index for processed foods and feeds was 0.9%, partially reflecting the differential gains in productivity.[12] The consumer may then substitute the less expensive agricultural products for fishery products, and the share of the total food markets will decline for fish. This is reflected in the data that show 0.8 and 3.6% increase in per capita consumption of meat and poultry, respectively, while the per capita consumption of fish remained constant over the 1960-69 period.

Data are not readily available on fishing labor productivity in other countries. For illustrative

[10] The aggregate productivity index based upon 18 fisheries will be used throughout the remainder of this article. Furthermore, we are comparing annual productivity in other sectors (as opposed to output per man-hour) with that in U.S. fisheries.

[11] Some have contended that the relatively lower price of poultry has resulted from a reduction in cost of feed. According to the Economic Research Service of the U.S. Department of Agriculture, feed grain and high protein feeds have increased over 31% over the last decade. Of course, technical improvements in genetics, breeding, nutrition, and feed formulation have increased feed conversion ratios in broilers, and this has been the proximate cause of the striking rise in labor productivity in the poultry industry. Hence, labor productivity is the prime factor or indicator which is used to assess the impact of changing technology in changing relative prices. This is the reason labor productivity is monitored so closely in each sector of the economy in our battle against inflation.

[12] Some have suggested that price support programs in agriculture have been a factor in lowering the price advance of agricultural commodities. Admittedly, agricultural price support programs have had an effect on agricultural prices, but the major effect has been reducing price fluctuations and stabilizing prices rather than a direct effect on the fundamental change in agricultural costs and price structures. Trends in any statistical series will depend to a certain extent on when the series is started. In the case of agriculture, prices were low in 1950 and picked up with the Korean conflict and dropped in 1953-54. Agricultural policy was to support prices starting in 1953-54—a continuation of their earlier policy in 1950. Prices in 1951-52, however, received little or no support. Consultation with the Economic Research Service of the U. S. Department of Agriculture indicated that the lower rate of advance in processed foods and feeds has been due to sizeable increases in agricultural production (from 1950), attributable largely to the rapid increase in agricultural labor productivity contrasted with a reduction in aggregate farm inputs (i.e., farm output grew at 1.8% per annum while inputs remained constant).

TABLE 3.—Comparisons of the growth rate in labor productivity for selected fisheries and countries.

Fishery	United States	Other country	Period[1]
Menhaden (Atlantic and Gulf of Mexico)	-0.4	[2] +2.8	1960-68
Northeast groundfish	-1.9	[3] +4.0	1959-69
Inshore American lobsters	-0.3	[4] −3.8	1959-69

[1] Periods are different than shown in Table 1 because of lack of data in foreign countries for earlier periods.
[2] Peruvian anchoveta.
[3] Canada.
[4] Canada.

purposes, however, we do have some information for the groundfish, menhaden, and lobsters as shown in Table 3. For this limited sample, it is quite apparent that U.S. fishermen are *not* holding their own with their foreign counterparts in menhaden and groundfish. More research is needed in this area.

FACTORS BEHIND THE GROWTH IN LABOR PRODUCTIVITY IN FISHING

Why has labor productivity increased at a lower rate in fisheries than in competing sectors such as meat and poultry? Has it been because fishermen are technologically backward or are not working harder? To answer these questions, we have selected three fisheries for examination. As indicated in the introduction, there are many factors that influence the trends in the productivity of fishermen. Probably, there are two important opposing forces. First, fishermen attempt to improve their technology, training, and experience so that their capability to catch fish will be enhanced. This tends to raise productivity. Second, the fishermen, unlike their counterparts in agriculture, are characterized by finite limitations to production. The buildup of aggregate fishing effort (i.e., vessels, gear and fishermen) tends to lower the productivity (catch per unit of effort) of those fishing the resource because more people share a fixed pie. This is a paradoxical result in that improvements in technology increase gear efficiency but also increase effective fishing effort, which in turn depresses the catch per unit of effort. Unless the level of effective fishing effort is controlled (e.g., through limited entry and not merely making gear less efficient or maintaining constant gear efficiency), the fishermen will remain on a constant treadmill attempting to balance changes in technology against the finite productivity of the resource. This is why fishery management may be one of the more important solutions to the problem. In addition there are other factors that influence labor productivity in the fisheries such as changes in the environment and institutional changes (e.g., gear regulations).

In an attempt to quantify the influence of these important factors on labor productivity, for each fishery we computed the statistical relation between annual landings per fisherman and the following factors:

1. Aggregate fishing effort
2. Fishing effort per fisherman
3. Secular time trend
4. Environmental factors
5. Institutional or regulatory changes.

It is hypothesized that increases in *aggregate* fishing will depress productivity; increases in fishing effort per worker (e.g., traps fished per fisherman, standard days fished per fisherman, or other gear used per fisherman) will increase productivity; a secular time trend represents all other factors such as changes in technology that may raise productivity; environmental change may either raise or lower productivity depending on individual factors; and regulatory changes will hopefully raise productivity.

Eastern Tropical Pacific Yellowfin and Skipjack Tuna

The fishery for tropical tunas in the eastern Pacific Ocean developed shortly after the turn of the century. The degree of exploitation increased steadily as the U.S. fleet, which lands the major portion of the catch, grew, and as the fleets of Latin America and Japan developed. Prior to 1959, the catch of yellowfin and skipjack tunas from the eastern tropical Pacific Ocean was taken by bait fishing vessels that use live bait and pole. After 1959, many fishermen converted their bait vessels to purse seiners

which have subsequently proved to be more efficient fishing vessels. Over the 1935-69 period, annual landings per tuna fisherman showed an upward time trend, growing at a rate of 2.1% per year.[13]

To analyze the growth in labor productivity in the eastern tropical Pacific tuna fishery, we specified the following explanatory variables: fishing effort, or the aggregate number of standard fishing days; fishing effort per worker (i.e., standard units of fishing effort expended per worker); secular trend variable; crew size; and a variable to reflect any residual increase in labor productivity because of the switch from bait fishing to purse seining.[14] As expected, the statistical analysis revealed that the buildup in fishing effort displayed a negative impact on labor productivity; fishing effort per worker exhibited a positive influence on labor productivity; and the other factors were not statistically important. The Inter-American Tropical Tuna Commission apparently did a good job in adjusting its effort series for the switch in technology over the 1960-67 period. Therefore, it must be concluded that the switch in technology is primarily reflected in the effort-per-worker variable. A look at the effort-per-worker series reveals that it increased from approximately 13 to 20 standard units of effort per worker from 1959 to 1960. Prior to 1959, the standard unit of fishing effort per worker increased gradually, owing presumably to more efficient use of labor in searching and catching tuna. Although fishing effort increased appreciably over the period, its negative effect was greatly offset by increases in effort per fisherman, resulting in an annual growth rate of 2.1% over 1935-69. The actual and computed (using a statistical equation) yellowfin landings per fisherman are shown in Figure 3.

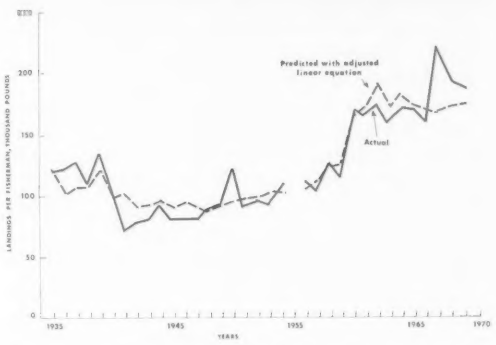

FIGURE 3.—Observed and predicted labor productivity (annual landings per fisherman) for the eastern tropical Pacific tuna fishery, 1935-54 and 1956-69. Estimating equation: $Q/L = -50615 - 2.524E + 7406E/L + 13501L/K$. Variables: E = effort in fishing days; E/L = effort per fisherman in days; L/K = crew size. R^2 = 0.82; D-W = 1.22; t values—E = 2.81; E/L = 8.04; L/K = 1.76. Annual compound rate of growth = 2.1%. Data source: Inter-American Tropical Tuna Commission.

Pacific Halibut

Early commercial fishing for Pacific halibut is considered to have commenced in 1888 when three sailing vessels from the New England States started to fish Cape Flattery on the northwest coast of Washington Territory. The rapid development of the Pacific halibut fishery did not occur until the 1920's. Initially, the fishery for the larger vessels was conducted over 12 mo of the year. Because of the possibility of overfishing, the season was legally restricted by a 3-mo winter closure in 1924. Since then the season has been regulated by the International Pacific Halibut Commission (IPHC). The fishery is presently carried on by a mixture of Canadian and U.S. longline vessels.

Unlike other fisheries, an analysis of changes in labor productivity is complicated by institutional factors (i.e., control by IPHC of gear and length of season) as well as economic and biological forces. Considering the entire fishery, it is hypothesized that annual labor productivity is heavily influenced by the following factors:

1. Length of fishing season
2. Aggregate fishing effort
3. Fishing effort per worker
4. Crew size on halibut vessels
5. Secular time trend.

In the Pacific halibut fishery, we used average landings per man-day at sea as a measure of

[13] Catch quotas of yellowfin tuna were not a factor in productivity until 1969.

[14] The number of fishermen employed is a series which was estimated by Bruno G. Noetzel of the Economic Research Division with the help of material published in various years of the Annual Report of the Inter-American Tropical Tuna Commission.

labor productivity.[15] Over the 1927-68 period, landings per fisherman-day increased by 2.5% a year. The use of landings per fisherman-day eliminates the influence of shorter seasons due to regulations. According to the IPHC, an adjustment has already been made to the effort series to include improvement in technology. Therefore, the time trend will reflect any residual influence of secular improvement in labor productivity not specifically measured as part of the effort series. In addition, since the skates series[16] is really a skates-per-day series, we can create a fishing-effort-per-worker series. This would measure the amount of fishing effort exerted per worker and should have a positive influence on labor productivity, holding other factors constant. The statistical results reveal that both fishing effort and gear used per worker are statistically important determinants of productivity and exhibit the hypothesized sign. Crew size and the time trend were not statistically important. Figure 4 shows the actual and computed annual landings per fisherman-day in the Pacific halibut fishery.

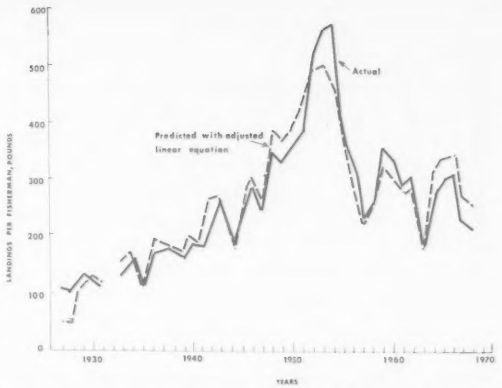

FIGURE 4.—Observed and predicted labor productivity (landings per fisherman *day*) for the Pacific halibut fishery, 1927-31 and 1933-68.
Estimating equation: $Q/(L \times S) = 50.654 - 0.254(E_2 + E_3) + 167.161\ (E_2' + E_3')/(L \times S) + 2.112\ T$. Variables: $(E_2 + E_3)$ = total effort in number of skates; $(E_2' + E_3')/(L \times S)$ = U.S. effort per fisherman day in number of skates; T = secular trend. $R^2 = 0.91$; D-W = 0.66; t values—$(E_2 + E_3) = 4.41$; $(E_2' + E_3')/(L \times S) = 12.71$; $T = 2.99$. Annual compound rate of growth = +2.5%. Data source: International Pacific Halibut Commission.

The Inshore American Lobster Fishery

The inshore American lobster fishery is largely based upon fishing with wooden traps or pots; most lobsters are caught off the coast of Maine. Based upon previous studies such as that done by Dow (1961), it was hypothesized that changes in lobster productivity are due to the following factors:

1. Total number of traps fished per annum
2. Traps fished per fisherman
3. Crew size
4. Mean annual seawater temperature, Boothbay Harbor, Maine
5. Secular time trend.

According to our statistical analysis, the secular decline in seawater temperature and increase in aggregate fishing effort produced a decided negative effect on labor productivity. The computed and actual labor productivities are shown in Figure 5. Holding all other factors constant, the *increase* in fishing effort and secular *decline* in seawater temperature lowered annual landings per fisherman. However, increases in fishing effort per fisherman and the secular trend offset the negative factors, thereby producing a negligible downward trend in lobsterman productivity. In conclusion, despite drastic changes in fishing effort and seawater temperature in the inshore American lobster fishery, labor productivity did not change appreciably over the 1950-69 period.

MAJOR FINDINGS

1. Of the 17 fisheries studied, 11 exhibited positive time trends in output (landings) per fisherman. Based upon available data, therefore, it is quite apparent that many sectors of the fishing industry experienced substantial increases

[15] This variable was formed by dividing the actual annual halibut catch by an estimate of the number of man-days expended in producing that catch. The estimate was derived by multiplying the halibut employment by the average number of days in a halibut season per annum.

[16] In Pacific halibut, fishing pressure is measured in terms of a skate of setline gear. "The groundline in a skate of gear is usually 250 to 300 fathoms long. Short lines called gangions are attached to the groundline at regular intervals and each gangion carries a hook." (Skud, 1972, p. 5).

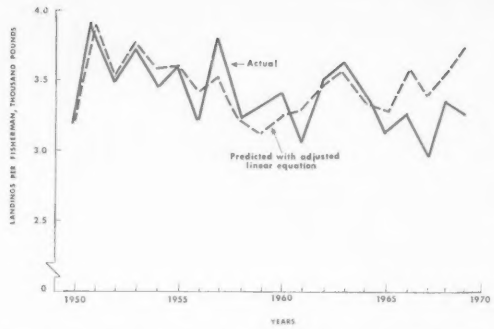

FIGURE 5.—Observed and predicted labor productivity (annual landings per fisherman) for the inshore American lobster fishery, 1950-69. Estimating equation: Q/L = -1290 - 0.003 E + 16.886 E/L - 2840L/K + 158.435° F + 76.930T. Variables: E = number of traps fished; E/L = traps fished per fisherman; L/K = crew size; °F = seawater temperature; T = secular trend. R^2 = 0.69; D-W = 2.20; t values—E = 2.15; E/L = 1.73; L/K = 1.60; °F = 2.99; T = 1.85. Annual compound rate of growth = -0.5%. Data source: Fishery Statistics of the United States.

in labor productivity over the 1950-69 period. Also, the annual fluctuation of labor productivity varied significantly among the fisheries from the Gulf of Mexico blue crab to the North Atlantic groundfish fisheries.

2. The construction of a productivity index for *all* fisheries indicated that, for U.S. fisheries as a whole, labor productivity increased by approximately 2.5% per year over 1950-69. The growth rate slackened, however, in recent periods.

3. Of great importance, labor productivity in the U.S. fishing sector grew at a lower rate (i.e., 2.5%) than the entire U.S. economy. However, it was significantly below levels of labor productivity advances in poultry (9.8%) and meat (3.8%), which are fish's chief competitors for the consumer's protein dollar. Preliminary international comparisons revealed that U.S. advances have not been keeping pace with labor productivity advances in other countries for the groundfish and menhaden fisheries.

4. In our detailed study of three selected fisheries, it was generally found that two forces were at work: (a) increasing pressure on the resource base and (b) attempts to increase the fishing effort per worker. We were successful in isolating the quantitative effect of each factor. Generally, it was found that increases in fishing effort per worker offset the negative impact of rising aggregate fishing effort on the resource, thereby producing a rise in output per fisherman over the period of analysis. We were also quite successful in identifying the quantitative impact of such other productivity determinants as environmental, technological, and regulatory factors. The productivity function developed to explain changes in output per fisherman were quite successful in explaining the trend in the actual data.

ACKNOWLEDGMENT

We are greatly indebted to Fred Olson of the Economic Research Division for his helpful comments and suggestions dealing with the comparisons between fishing and agricultural productivity made in this article.

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APPENDIX

Employment Figures in the U. S. Fishing Industry

The employment data utilized are from "Fishery Statistics of the United States" compiled by the Division of Statistics and Market News, National Marine Fisheries Service. The numbers of fishermen employed separated by the type of fishing craft they work. The number of fishermen on vessels are gathered by field personnel

through interviews, while fishermen on boats (craft of less than 5 net tons) are obtained from State conservation agencies through licensing and by contract with firms purchasing fish or shellfish from fishermen.

Except for problems of duplication brought about by fishermen and fishing craft shifting from one fishery to another and from one region to another, the Division of Statistics and Market News report data on total numbers are very reliable. Problems arise when one is interested in the time spent in fishing by fishermen and their craft. The number of hours, days, weeks, or months worked is not reported. Most fisheries are highly seasonal, lasting as little as several weeks, while others are year around, although they may have seasonal peaks.

Except for Pacific halibut, the number of fishermen is the total number engaged in fishing regardless of the fishing craft employed, and length of employment. In most areas, fishermen not on vessels have been divided into regular and casual. Regular fishermen are defined as those who receive more than one-half their annual income from fishing, whereas casual are those who receive less than one-half their earnings from fishing. It has not been possible to separate regular from casual fishermen on the Pacific coast. When information on casual or part-time fishermen was available, the ratio of part-time to full-time fishermen was tested by including it as an independent variable in "explaining" changes in labor productivity. The variable was significant in only two fisheries, indicating the higher percent of part-time fishermen tended to lower annual landings per fishermen.

Therefore, although the employment figures are somewhat less than optimal and the reader should be warned against many of these data problems, the rate of growth in labor productivity published in this article is probably fairly accurate. For a further discussion of these problems, the reader may write the Economic Research Division, National Marine Fisheries Service, NOAA, U.S. Department of Commerce, Washington, D.C. 20235 for a draft manuscript entitled "The Measurement and Analysis of Labor Productivity Changes in United States Fisheries."

EFFECT OF p,p′-DDT ON DEVELOPMENTAL STABILITY OF PECTORAL FIN RAYS IN THE GRUNION, *LEURESTHES TENUIS*

DAVID W. VALENTINE[1] AND MICHAEL SOULÉ[2]

ABSTRACT

Experiments are described that test the validity and utility of using bilateral asymmetry for the early detection of environmental deterioration. The first experiment, using a continuously flowing water system, was designed to test the effects of a ubiquitous pollutant, p,p′-DDT, on the pectoral fin ray asymmetry of grunion, *Leuresthes tenuis*, fry. Toxicant concentrations ranged from a low of 0.001 to a high of 500 parts per billion. The two highest p,p′-DDT concentrations, 100 and 500 parts per billion, proved lethal to grunion fry. For the other concentrations, increases in pectoral fin ray asymmetry with increasing toxicant concentration were observed. Increases in asymmetry were statistically significant.

The second experiment, which utilized a recirculating static water system, was designed to determine inherent differences in the level of pectoral ray fin asymmetry in fish from different localities. Results for grunion fry paralleled previously published results for adult grunion. Grunion from the relatively polluted southern California region had higher asymmetry levels than did those from Baja California. The significance of these results as they relate to the general question of asymmetry as a statistical indicator of environmental stress is discussed.

Asymmetry of bilateral characters has been proposed as a morphological measure of environmental stress in fish populations (Valentine, Soulé, and Samollow, 1973). The theory underlying such an analysis is that various environmental stresses may reduce the efficiency of developmental homeostatic mechanisms, thus leading to an average increase in the within-individual variation of morphological structures (Adams and Niswander, 1967). An asymmetry index, then, might provide a relative estimate of the physiological stress to which a population is being subjected.

Data from three wild-caught fish species supporting this hypothesis have previously been presented (Valentine, Soulé, and Samollow, 1973). We now present experimental results supporting the theory.

METHODS AND MATERIALS

Grunion, *Leuresthes tenuis*, were chosen as our experimental organism. Grunion are small, rapidly maturing, marine atherinids endemic to the Californias. They possess many features which make them attractive as a laboratory organism. Grunion spawn biweekly on sandy beaches during the high tides from late February or early March through August or September, and wild-spawned eggs may be easily collected by digging in wet sand after such a spawning run. The eggs mature into fry in about 10 days (Walker, 1952). Fry are large and easily maintained in the laboratory.

The approximate straight-line distances in miles to the localities mentioned in this paper from Point Fermin, the prominent point located adjacent to the entrance of the Los Angeles Harbor, are Belmont Shore, 9; Del Mar, 87; La Jolla Shores, 91; San Diego, 101; and Bahia San Quintin, 270. All of these localities are south of Point Fermin.

The toxicant chosen was p,ṕ-DDT(1,1,1-trichloro-2,2-bis(p-chlorophenyl) ethane), the metabolic products of which are known to be ubiquitous in the world ecosystem (Risebrough, Hugget, Griffin, and Goldberg, 1968). Such compounds are found in fairly high concentrations in marine organisms from California waters

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FISHERY BULLETIN: VOL. 71, NO. 4, 1973.

(Risebrough et al., 1967; Anas and Wilson, 1970; Wolman and Wilson, 1970; Burnett, 1971; Shaw, 1971, 1972; Castle and Woods, 1972; Munson, 1972; Risebrough, Menzel, Martin, and Olcott[3]).

Two types of apparatus were used: a flowing water system and a static water system. The flowing water apparatus was used for experiments in which fish were subjected to different toxicant concentrations. Flowing water mitigates differential toxicant uptake in experimental aquaria where unequal numbers of organisms are present. The static water apparatus was used to examine differences in congenital (untreated) asymmetry in populations; it employed filters to remove metabolic by-products.

Flowing Water Experiments

The experimental apparatus used consisted of 10 pairs of 6-liter, solid, molded, all-glass aquaria. One pair of aquaria was used as a control, the other nine pairs had the following p,p′-DDT concentrations: 0.001, 0.01, 0.1, 0.4, 0.7, 1, 10, 100, and 500 ppb (parts per billion). Water was gravity-fed from an 18-liter seamless all-glass reservoir tank to a pair of aquaria, thus ensuring that each experimental pair received the same quantity of toxicant. Water levels in the aquaria were maintained at 4 liters by individual all-glass, air-lift water pumps, each pump having the capacity to remove more water from the aquaria than was entering from the reservoir. Aquaria were covered with a ¼-inch plastic cover, and air was removed by vacuum (discharged to the outside of the building) to prevent contamination between tanks. Waste water from each tank was discharged into a central collecting tube and deposited into a sealed drain. The water flow to each tank was such that its water was completely replaced daily.

To obtain the desired toxicant concentrations, as mentioned above, standard solutions of p,p′-DDT in pesticide quality acetone were prepared. The quantity of p,p′-DDT in each standard solution was such that when 100 μl of acetone was dissolved in 18 liters of seawater (the size of our reservoir tanks), the concentration of p,p′-DDT in each reservoir tank was brought to one of the desired experimental concentrations. Filtered seawater was used for these experiments (obtained from the Scripps Institution of Oceanography Aquarium supply).

Grunion eggs for this experiment were collected from Belmont Shore. The eggs were obtained by digging in the sand the morning after a major grunion run. Clutches of eggs were placed in damp sand for an incubation period of 10 days. Eggs were hatched by placing handfuls of egg-bearing sand in seawater and agitating for a short period of time.

The flowing water experiments were begun with two control tanks and two replicate tanks for each treatment. Each tank initially contained approximately 400 fry. Thirty-eight days after hatching (48 days after being spawned), fish in one of the control tanks and one each of the replicate treatment tanks were killed. Fifty-one days after hatching (61 days after being spawned), the remaining fish were killed.

Static Water Experiments

The static water experiments consisted of raising grunion fry from different localities in continuously filtered recirculating seawater. Seawater in these tanks was changed weekly. Approximately 400 fry were used from each of three localities, Belmont Shore, Del Mar, and Bahia San Quintin, 200 fry being placed in each of two replicate tanks. Collection of eggs, hatching, and experiment termination periods were identical to those previously described.

All grunion were fed several times weekly on a diet consisting of newly hatched brine shrimp nauplii. Dead brine shrimp were removed from all tanks daily. Water temperature was ambient (ca. 20°C). No attempt was made to adhere to a light-dark cycle.

Analyses

Upon termination of each experiment, live

[3] Risebrough, R. W., D. B. Menzel, D. J. Martin, and H. S. Olcott. 1970. DDT residues in Pacific marine fish. Unpubl. manuscr., 32 p. Bodega Bay Mar. Lab., Bodega Bay, CA 94923.

specimens were placed in a 10% Formalin[4] solution. The fish died with their pectoral fins spread. After a minimum of 24 h in the fixative, specimens were rinsed in fresh water and stained for several hours in a 5% KOH-alizarin red solution. Pectoral fin rays were scored using a binocular dissecting microscope. The standard length of each specimen was determined by placing individuals on a flat plastic ruler.

We have chosen to use the variance, V_a, of the right (R) minus left (L) values to quantify the amount of asymmetry. This statistic is simply $\Sigma(d - \bar{d})^2/N - 1$, where d is an individual's asymmetry (right minus left value), $\bar{d}$ is the mean of the asymmetry distribution, and N is the sample size. In our previous paper we used a similar statistic, the squared coefficient of asymmetry variation,

$$CV_a^2 = (s_d \times 100/\bar{x}_{R+L})^2,$$

where the scale correction, $\bar{x}_{R+L}$, is the mean value of the character itself. In contrast to the earlier study, we found that the amount of asymmetry was uncorrelated with the mean character state, probably because the fins of the grunion in this study were still developing. Even though smaller grunion fry had fewer fin rays, they were not less asymmetrical in an absolute sense.

The use of CV_a^2 would, in fact, give misleading results. For example, examination of Table 1 will show that fry in untreated tanks have pectoral fin ray means varying from a low of 13.491 (Control) to a high of 23.220 (Del Mar). The V_a values are 0.554 and 0.596, respectively. The corresponding CV_a^2 values are 30.5 and 11.0.

RESULTS

One-half of the replicates were killed at 38 days after hatching because we were uncertain how long the fry would live. The remaining replicates were terminated 51 days after hatching. This latter time period was chosen because examination of grunion fry from Bahia San Quintin at that age (this experiment was started 2 wk before the others) indicated that the number of pectoral fin rays was near the same mean as was found in wild adults. Mortality, due to an unknown cause, was also reducing the numbers of fry in some tanks. The 38-day experiments were terminated too early to yield useful data as many fish had not yet begun to develop ossified pectoral fin rays.

Grunion fry receiving the largest dose of p,p'-DDT, 500 ppb, began showing signs of neuromuscular dysfunction the day after the experi-

[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Grunion statistical information.

Treatment	N	Mean length ± standard error	Pectoral fin rays: Mean count (right + left) ± standard error	Pectoral fin rays: [1] V_a
Static water experiments				
Bahia San Quintin	75	13.811 ± 0.084	22.800 ± 0.332	0.132
Del Mar	82	14.734 ± 0.096	23.220 ± 0.267	0.596
Belmont Shore	79	12.457 ± 0.099	16.684 ± 0.296	0.590
Flowing water experiments				
Control[2]	53	11.728 ± 0.122	13.491 ± 0.557	0.554
0.001 ppb DDT	66	12.625 ± 0.105	20.303 ± 0.381	0.519
0.01 ppb DDT	7	13.486 ± 0.531	22.714 ± 1.266	0.576
0.1 ppb DDT	64	12.358 ± 0.114	19.031 ± 0.442	1.499
0.4 ppb DDT	65	12.602 ± 0.127	20.154 ± 0.473	0.898
0.7 ppb DDT	78	12.096 ± 0.088	17.679 ± 0.384	0.918
1.0 ppb DDT	51	11.402 ± 0.137	11.409 ± 0.737	2.401
10.0 ppb DDT	65	12.409 ± 0.139	18.985 ± 0.606	2.902

[1] Asymmetry variance.
[2] Control for the flowing water experiments.

ment began. Fry began swimming erratically, moving jerkily and, unlike untreated fry, swam on or near the bottom of the tank, sometimes upside down. Within a week all fry died. After 1 wk, fry in the 100-ppb treatment tanks began showing similar signs. Mortality reached 100% after 2 wk.

Asymmetry data are presented in Table 1. Grunion from Bahia San Quintin have the lowest variance of all groups examined. Fish from Del Mar and Belmont Shore, as well as the Control 0.001 and 0.01 fish, have intermediate variances (the 0.01-ppb sample should perhaps be eliminated because of its small size). Slightly greater variances are found in the 0.1-, 0.4-, and 0.7-ppb treatments. Finally, the 1- and 10-ppb treatment fish have the highest variances. It should also be pointed out that while the progression of asymmetry variances for p,p'-DDT-treated fish in the flowing water experiments is not perfect, the trend is statistically significant. Applying the Tau coefficient (Sokal and Rohlf, 1969) to these data (Control through 10-ppb treatment) yields $0.05 > P > 0.02$.

Comparing the V_a values for fry from Belmont Shore and Bahia San Quintin with the V_a values for adult fish (from data presented by Valentine, Soulé and Samollow, 1973) indicates that the ratio of asymmetry for adults is nearly the same as it is for fry (Table 2).

Belmont Shore grunion contain almost twice as much DDT as do La Jolla Shores grunion: Belmont Shore females 2.45 ppm ± 0.97, $N = 5$; La Jolla Shores females 1.40 ± 0.77, $N = 2$ (values on a whole body, wet weight basis, and include all isomers and metabolic products). DDT values reported here for Belmont Shore fish were obtained from specimens caught during the first grunion run of the season, whereas the experimental eggs were collected almost 6 wk later, from the third run.

Circumstantial evidence supports the hypothesis that eggs spawned early in the season have relatively high levels of DDT. Walker (1952) states that older fish spawn first. If larger fish have higher body burdens of DDT than smaller fish, then eggs spawned by large fish might have more DDT. Alternatively, if the amount of DDT deposited in eggs is a constant proportion of the amount of DDT in the female body, then the first spawn would contain more DDT in absolute terms than the later spawns. We lay some stress on these possibilities because of our enigmatic observation that eggs from the first Belmont Shore run all failed to hatch, dying at an advanced stage of development.

If DDT increases asymmetry, then the low V_a values for grunion fry from Bahia San Quintin might be attributed to low adult and egg DDT burdens. Although we have no data on pesticides concentrations in adult grunion from Bahia San Quintin, we have gathered such data in barred sand bass, *Paralabrax nebulifer* (pertinent life history data for this species are given in Valentine, Soulé, and Samollow, 1973). DDT concentrations in barred sand bass from Bahia San Quintin are 0.199 ± 0.038 ppm (N = 16), from San Diego, 2.150 ± 0.184 ppm (N = 28), a difference of roughly an order of magnitude.

TABLE 2.—Comparison of pectoral fin ray V_a values for experimental and wild-caught grunion.

Locality	Wild adults			Experimental fry (untreated)		
	Date	N	V_a	Date	N	V_a
Bahia San Quintin	1970	57	0.070	1972	75	0.132
Belmont Shore	1969-70	27	0.286	1972	79	0.590

DISCUSSION

Egg and Adult DDT Burdens

We have measured the chlorinated hydrocarbon body burdens of several wild-caught grunion. These data will be published in a later paper and are here offered only for comparative purposes. Our small sample suggests that Bel-

DDT and Asymmetry

In our earlier report we showed that adult grunion from Belmont Shore were 4.08 times as asymmetrical as San Quintin fish. In the present study, the ratio of asymmetry variances in untreated fry is almost the same, 4.46. This consistency may be more than coincidence. This result and our experimental data support our hypothesis based on data from wild-caught fish that environmental stress may produce statistically detectable changes in asymmetry (Valentine, Soulé, and Samollow, 1973). Perhaps the most important result is that extremely low concentrations of DDT (< 1 ppb) cause a very significant deterioration in the symmetry of fin rays. When it is noted that in all probability the control fry from Belmont Shore were already carrying a stressful load of DDT, the significance of the results is enhanced.

Our rationale for utilizing p,p'-DDT as a stressant was that it (and its metabolic products) are known to occur in high concentrations in southern California marine organisms (Burnett, 1971; Castle and Woods, 1972; Duke and Wilson, 1971; Munson, 1972; Risebrough et al., 1967). The White's Point outfall, situated about a mile north of Point Fermin, was shown to be releasing effluent containing DDT approaching 100 ppb in late 1970, and also similar quantities of polychlorinated biphenyls (Schmidt, Risebrough, and Gress, 1971). These polychlorinated biphenyls may themselves produce increases in asymmetry since they have properties similar to DDT (Risebrough, Reiche, Peakall, Herman, and Kirven, 1968; Gustafson, 1970; Peakall and Lincer, 1970). We would, in any case, expect to find a diversity of agents in southern California's marine waters capable of producing increases in asymmetry, among them DDT.

Grunion fry exposed to increasing levels of p,p'-DDT in water yielded results in accord with our environmental stress hypothesis (Valentine, Soulé, and Samollow, 1973). At p,p'-DDT levels greater than 0.01 ppb, asymmetry values increased. Increases in the asymmetry of bilateral structures are easily quantified and monitored. We hope other workers will test this system with other pollutants that may affect calcium metabolism. The funding situation precludes our doing so.

ACKNOWLEDGMENTS

We dedicate this paper to our colleague, E. W. Fager, a constructive and creative critic and a good friend. This research was supported by a contract from the Southern California Coastal Water Research Project (NO. 02304). The second author, Michael Soulé, was supported by National Science Foundation Grants GB-27358 and GB-8525.

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ACANTHASTER (ECHINODERMATA, ASTEROIDEA) IN THE GULF OF CALIFORNIA

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ABSTRACT

Possible invasion of the coral-rich Caribbean by eastern Pacific populations of *Acanthaster*, which might follow on construction of a sea-level Central American canal, directed our attention to *Acanthaster* in the Gulf of California. Based on the literature, field notes, and a study of tagged specimens, the distribution, density, and behavior of this little known asteroid are discussed.

The population extends through some 300 miles of the southern half of the Gulf, mainly along the western shore, and appears to be geographically isolated from eastern Pacific *Acanthaster* populations known at lower latitudes. It is sparse and, even where common, average density estimates are of the order of 1/200 m^2. Through the northern part of its range, the sea star feeds primarily on small encrusting growths of *Porites californica*, but in the most southerly regions, *Pocillopora* is a frequent prey. The change in prey preference appears to be related to the distribution of the coral species and to changes in their dominant growth forms.

During a 48-h study of nine tagged specimens, 70% of the observed activity involved feeding, 20% resting, and 10% traveling. There was no clear-cut diurnal behavior, and no tendency to aggregate or to migrate as a population.

Measurements and behavioral traits indicate that *Acanthaster ellisii* is a valid binomen for the Gulf of California. We conclude that, if there is ground for concern over transoceanic invasion, it should shift to the more southerly population.

The alarm which followed early reports (Barnes, 1966; Endean, 1969; Chesher, 1969) of the devastation of South Pacific coral reefs by the crown-of-thorns sea star, *Acanthaster planci*, appears to have subsided, although interpretation of the phenomenon is still being debated (Dana, 1970; Newman, 1970; Vine, 1970; Weber and Woodhead, 1970; Dana, Newman, and Fager, 1972). However, the events have served to highlight our ignorance of the eastern tropical Pacific representatives of the genus. Furthermore, the possible construction of a Central American sea-level canal through which eastern Pacific *Acanthaster* might gain access to the coral-rich, but *Acanthaster*-free tropical Atlantic, has raised the question of the predation-potential of the American population (Newman and Dana, in press; David Pawson, pers. comm.).

The long-standing questions surrounding the taxonomic status of *Acanthaster* in the Gulf of California and adjacent regions have been further confused by the discovery of large numbers in the Secas and Contreras Islands adjacent to the Gulf of Panamá (Glynn, 1970a, b; 1972), and it is not at present clear whether any or all of the American *Acanthaster* are assignable to *A. ellisii* (Gray, 1840), to *A. ellisii pseudoplanci* Caso, 1962, or to *A. planci* (L., 1758). However, we consider *A. ellisii* a valid binomen for the populations we have observed in the Gulf of California, and shall adhere to it for purposes of this report.

As recently as 1955, *A. ellisii* was known from less than a dozen lots, mostly of single

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TABLE 1.—Numbers, distribution, and feeding behavior of *Acanthaster ellisii* in the Gulf of California.

Location	Reference[1]	Stations	Date	Number of specimens	Observation		
					Not feeding	Feeding	Prey
B. San Carlos	1	S side, Pta. Dobles	Jan. 1966	1	No data		
Pta. Sta. Inez	1	SW side	Nov. 1966	Few	No data		
Pta. Sta. Inez	1	SW side	July 1967	Few	No data		
Pta. Sta. Inez	1	SW side	Nov. 1968	Few	No data		
Pta. Concepción	1	1 mile S of B. Concepción	Nov. 1966	Few	No data		
Pta. Concepción	1	1 mile S of B. Concepción	Nov. 1968	Few	No data		
Pta. Concepción	1	1 mile S of B. Concepción	Nov. 1970	2	0	2	*Porites*
Pto. Escondido	1	SW side, Coyote Pt.	Nov. 1966	Few	No data		
Pto. Escondido	1	SW side, Coyote Pt.	Nov. 1968	Few	No data		
Pto. Escondido	1	SW side, Coyote Pt.	Nov. 1970	5	0	5	*Porites*
I. San Ignacio	1	SE side	Mar. 1971	1	0	1	*Porites*
I. San José	2	Stn. 6, SW end	Apr. 1970	5	3	2	*Pacifigorgia* (1); *Padina* (1)
I. San José	3	Stn. 6, SW end	Oct. 1971	3	No data		
I. San Francisco	4	Stn. 4, cove on S side	Apr. 1970	12	6	6	*Porites*
I. San Francisco	3	Stn. 4, cove on S side	Oct. 1971	12	7	5	*Porites*
I. San Francisco	4	Stn. 3, SW anchorage	Apr. 1970	7	No data		
I. San Francisco	2	Stn. 1-5, S side	Apr. 1970	48	Incomplete, but:		*Porites* (30); *Pacifigorgia* (1)
I. Partida	1	Pink Cliff station	Nov. 1970	4	[2]4	[2]12	*Porites*
I. Partida	1	Pink Cliff station	Mar. 1971	9	[2]18	[2]38	*Porites* (30); *Pocillopora* (2); coralline algae (2); ? (4)
I. Partida	4	Stn. 1, SW end	Apr. 1970	1	No data		
I. Partida	3	Stn. 2	Apr. 1970	1	[2]	No data	
I. Partida	3	Stn. 2	Apr. 1972	2	2		
I. Partida[3]	2	Stn. 7, 8 SW end	Apr. 1970	16	0	16	*Porites* (14); *Psammacora* (1); *Pocillopora* (1—presumed)
I. Espíritu Santo	2	Stn. 10, in B. San Gabriel	Apr. 1970	1	0	1	*Pocillopora* (1—presumed)
I. Espíritu Santo	3	Stn. 7, N. side San Gabriel	Oct. 1971	4	0	4	*Pocillopora*
I. Espíritu Santo	3	Stn. 7, N. side San Gabriel	Apr. 1972	2	1	1	*Pocillopora*
Ens. de los Muertos	3	Stn. 8, NW side P. Arena	Apr. 1972	9	4	5	*Pocillopora* (4); *Porites* (1)
Cabo Pulmo	3	Stn. 9, seaward of inner reefs	Apr. 1972	3	2	1	*Porites*
B. Frailes	3	Stn. 10, NE side	Apr. 1972	1	0	1	*Pocillopora*

[1] 1 = Authors.
2 = Dana and Wolfson (1970).
3 = Faulkner, unpublished notes.
4 = Faulkner, cited in Dana and Wolfson (1970).
[2] Based on multiple observations of same specimens (See text and Table 3).
[3] Cited as Espíritu Santo.

specimens (Madsen, 1955). The fact that the sea star inhabits rocky subtidal substrates has made it generally unavailable to shore collectors and impossible to dredge; only with the increased use of diving techniques has it become accessible. Accordingly, the literature is sparse.

Since Madsen's review (1955), *A. ellisii* has been described and contrasted to *A. ellisii pseudoplanci* by Caso (1962), and Barham and Davies (1968) and Glynn (1972) have mentioned it. Only Dana and Wolfson (1970) have dealt with any aspects of its biology. It is apparent from recent field observations (Dana and Wolfson, 1970; D. J. Faulkner, pers. comm.; and the material to be presented here) that the scanty records reflect our poor knowledge of the invertebrate fauna of the Gulf of California, rather than the prevalence of the sea star. This paper aims at adding to our understanding of the habits and habitats of *Acanthaster* in the Gulf of California.

We present information based on three distinct types of observations: 1) Presence and absence of *A. ellisii* noted in the course of our ecological surveys in the Gulf of California between 1965 and 1968, prior to a defined interest in the species; 2) numbers of *A. ellisii* and its prey observed by us at various locations during specifically directed surveys in November 1970 and by D. J. Faulkner in 1970, 1971, and 1972; 3) studies of tagged specimens at "Pink Cliff" station, Isla Partida, in November 1970 and March 1971.

Distribution of *Acanthaster* in the Gulf of California

The early records contribute little information on distribution. According to Madsen (1955), the collection site of Gray's type specimen was simply given as South America, and the two specimens described under the name of *ellisii* by Perrier were of unknown origin. Verrill (1869) listed La Paz as the locality for his *A. ellisii*, but the reference may be to the port from which it was shipped (Squires, 1959), and it was probably collected elsewhere. Thus, prior to 1970, the only valid records for *Acanthaster* in the Gulf of California are for Puerto Escondido, where Steinbeck and Ricketts (1941) collected several specimens, and where Madsen's (1955) type specimen was taken by an Allan Hancock Expedition. Some of Caso's specimens were also collected there by an Allan Hancock Expedition in 1940 (Caso, 1962).

Table 1, showing the distribution patterns of *A. ellisii* in the Gulf of California, combines our notes, the data given by Dana and Wolfson (1970), and the information contributed by Faulkner (cited in Dana and Wolfson, 1970). The known range of the species, extending through some 300 miles along the western shore of the Gulf of California, is shown in Figure 1.

No *Acanthaster* have been reported on the eastern shores of the Gulf, and our extensive search of the three areas which appear to offer suitable environments produced only two specimens: one at Bahía San Carlos, north of Guaymas, in January 1966 (we found none there in November 1968 and November 1970); the other, after a lengthy search, at Farallon San Ignacio. This small rocky islet offshore from Topolobampo represents one of the few likely environments for the asteroid for hundreds of miles along that part of the coast. No specimens were observed at the southeast end of I. Tiburon or on the adjacent mainland at Pta. Sargento.

Within its known range, *A. ellisii* is most often found on the south sides of islands and points, or in small embayments in the lee of northerly winds and partially protected from the south (Table 1). Note from Table 2, however, that although present at adjoining locations, it is not found in the more thoroughly protected bays and coves, such as Bahía Coyote, Pichilinque, and the inner bay at Puerto Escondido. Apparently the asteroid prefers habitats with some degree of wave action, but protected from violent wave shock and strong surge.

With two exceptions, there appears to be a good degree of correspondence in the distributions of *A. ellisii* and corals. The first exception is Bahía San Gabriel, where heavy growths of *Pocillopora* and other corals occur in a reeflike formation, and where Dana and Wolfson (1970) found only one *A. ellisii* in a thorough search of some 1,500 m^2. The second is El Pulmo, where by far the most extensive stands of branching

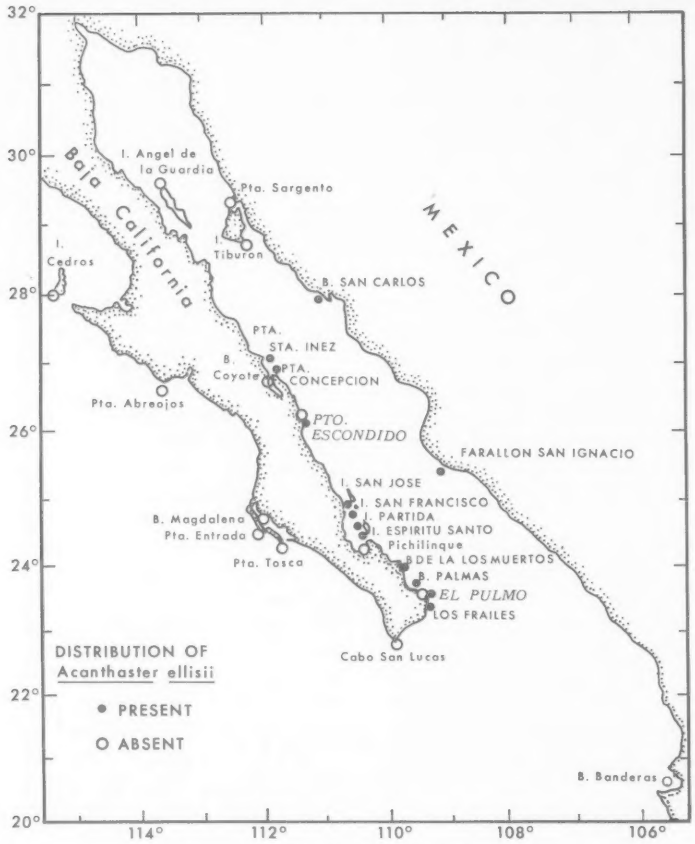

FIGURE 1.—Distribution of *Acanthaster ellisii*.

stony corals in the Gulf occur. We found no *Acanthaster* there on two visits, although we dove over large areas of the two shallower reefs and were towed behind a skiff over extensive regions of the deeper reefs. Sport divers have reported *A. ellisii* there, but the species is not easily identifiable on casual observation, and confusion with other asteroids, particularly with the similarly sized, heavy-spined, and abundant *Nidorellia armata*, is common. Faulkner's report (pers. comm.) of two specimens taken in relatively deep water outside the main reefs at El Pulmo represents an anomaly in the distribution of *A. ellisii* as otherwise observed.

Density

Except at the islands near La Paz (Islas San José, San Francisco, Partida, and Espíritu Santo, to which we shall refer as the "island complex") low densities of *A. ellisii* are suggested by the numbers in Table 1. Dana and Wolfson (1970) give 0.0045/m² (1/222 m²) for those islands, and the nine specimens we found in the thoroughly searched area of approximately 2,000 m² at "Pink Cliff" station on Isla Partida translate to an identical average. The high density at Pto. Escondido, 0.005/m² (1/200 m²), is deceptive, as we searched a preselected area where the sea stars were con-

TABLE 2.—Locations in the Gulf of California and adjacent areas where *Acanthaster ellisii* was not observed.

Location	Station	Date	Man hours underwater observation
Gulf of California			
I. Ángel de la Guardia	S. side of Arch Rock in P. Refugio	July 1967	8
I. Ángel de la Guardia	S. side of Arch Rock in P. Refugio	Nov. 1970	4
Pta. Sargento	SW side	July 1967	4
I. Tiburon	SE end	July 1967	4
B. San Carlos	S. side Pta. Dobles	Nov. 1968-Nov. 1970	16
B. Coyote	4 stations on or near I. Blanca	Nov. 1966	60
B. Coyote	4 stations on or near I. Blanca	July 1967	4
B. Escondido	Inner bay, S and E sides	Nov. 1966-Nov. 1968 Nov. 1970	8
P. Pichilinque	Bay on S. shore	Nov. 1966, Jan. 1968, Nov. 1968, Nov. 1970	50
B. Los Palmos	NW Shore	Jan. 1968	4
C. Pulmo	Lagoon and inner reef	Jan. 1968	6
C. Pulmo	Lagoon, inner and outer reefs	Mar. 1971	12
C. San Lucas	Sheppard's Rock area	Jan. 1965, Jan. 1968	20
West coast Baja California			
I. Cedros	SW end	Jan. 1965	8
Pta. Abreojos	SW end	Jan. 1965	2
B. Magdalena	NE shore	Jan. 1965	2
Pta. Entrada	Inside passage	Jan. 1965	8
Pta. Tosca	SW end	Jan. 1965	8
West coast Mexico			
Banderas Bay	5 stations E and S regions	Nov. 1968	40
Banderas Bay	1 station E region	Mar. 1971	4

centrated. The nine specimens reported by Faulkner (pers. comm.) at Ensenada de los Muertos constitute the only sizeable population known to the south of the La Paz island complex, but density figures are not available.

"PINK CLIFF" STUDY

Observations at Pink Cliff station provide an insight into the behavior of *A. ellisii*. We made preliminary observations there on four specimens in November 1970; a further study was conducted over a 48-h period in March 1971.

Study Area

The Pink Cliff study area covers about 2,000 m^2 in the northeast corner of El Cardonal Bay on the west side of Isla Partida (lat. 24°32′10″ N; long 110°23′30″W). The pink-pumice cliff extends about 3 m underwater and then curves into a wave-cut platform which interfaces at about 10 m with the sand bottom. Several large monument-like rocks with truncated tops stand isolated from the cliff. A few reeflike ledges lie farther seaward, and an extensive pile of large boulders is located near the northern edge of the platform. (Figure 2, based on underwater sketches and substrate measurements, gives a schematic picture of the area.)

Coralline algae predominate on rock and cliff faces. A rich growth of sessile organisms, dominated by sponges, tunicates, hydroids, and gorgonians, is concentrated on and near the vertical cliff and monument rocks. The upper rock surfaces and much of the platform are covered with a thin veneer of filamentous algal material. At the deepest levels, on the inshore sides of the rock pile, there is a luxuriant stand of the brown alga, *Padina*.

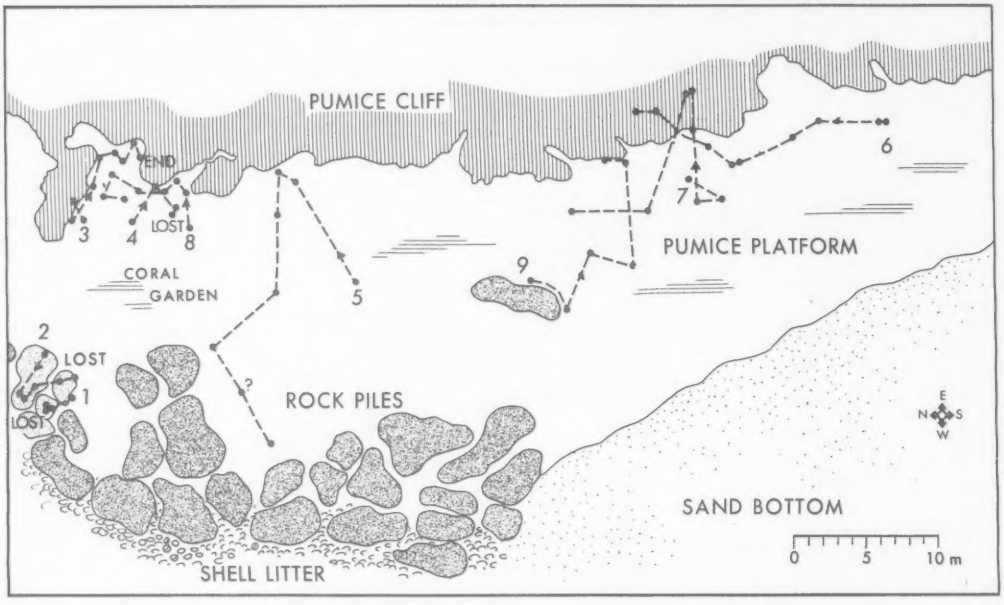

FIGURE 2.—Schematic diagram of Pink Cliff study area, Isla Partida, showing the relative positions and movements of the nine tagged *Acanthaster ellisii* during the 48-h study period. Depth of water at the interface between hard and soft bottoms is about 10 m.

Daytime underwater visibility in 1970 was about 20 m; in 1971, it varied between 6 and 15 m. Night visibility was reduced by swarms of mysids, polychaetes, and larval fishes which concentrated in the beams of our hand-held lights. Water temperatures were 27°C during the fall visit, 18°-21°C in the spring.

The Coral Fauna

Pocillopora is the conspicuous coral, although there are less than 20 large heads; the majority stand as scattered individuals in the "coral garden" near the cliff base in the northeast part of the platform. Several are inhabited by hawkfish (see Figure 3) and anomuran crabs. A few small *Pocillopora* grow on the lower vertical surfaces of the cliffs and monument rocks. Scattered small colonies of the dendrophyllid coral, *Tubastrea aurea*, are restricted to the deeply shaded sides of the monument rocks and cliff walls.

The large number of small encrusting *Porites californica* contradicts the first impression of a sparse coral fauna. In the deeper regions, these scablike coralla (see Figure 4) are about 4-5 cm in diameter and well separated from one another; with increasing height, they become progressively larger and less regular in outline, encrusting the pits and crevices, or covering small protuberances to form knobs.

The abundant *Porites* on the cliff face is so highly irregular in outline that it was impossible to distinguish individual colonies, but we attempted to count the coralla within a 0.5 m-diameter ring placed in five locations on each of two transects along the platform. Numbers increased from 50 coralla/m^2 on the seaward edge of the platform to 100 coralla/m^2 at the cliff base. In the surge shadow cast by a 3 m-high rock, and on the adjacent region of the platform which is protected from surge by the reef, there were as few as 10 coralla/m^2.

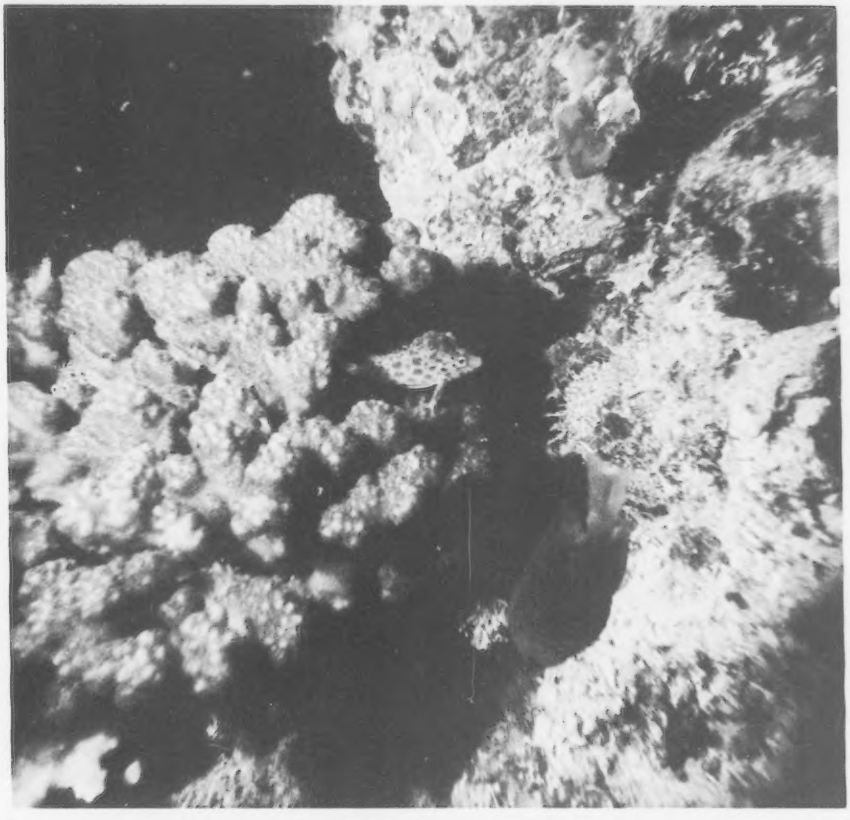

FIGURE 3.—An isolated head of *Pocillopora* sp. harboring two hawkfish (family Cirrhitidae), photographed near the base of a monument rock in the Pink Cliff study area. Only minor blemishes are evident on the distal regions of the branches.

Methods and Procedures

On 1 November 1970, we tagged four *Acanthaster ellisii* in situ by threading monofilament, to which numbered tapes were knotted, through the body wall and under the dermal ossicles with a curved upholstery needle. The operation was particularly awkward because of the necessity of wearing heavy gloves and entailed considerable manipulation of the animals, causing one specimen to react in an abnormal manner. The 16 observations made in this preliminary study are summarized in Table 1.

For the 1971 survey, the nine specimens located within the search area were tagged by simply tying numbered tapes to a ray (Figure 5). (This procedure also required great care and has additional drawbacks. If the monofilament is tied too tightly, the sea star may autotomize the insulated arm, as one of our specimens did after 40 h. Conversely, two loosely tied tags snagged and pulled free. Fortunately, they were found near animals whose characteristics corresponded to originally tagged individuals, and the tags were retied.)

The position of each specimen was marked with a short length (approximately 30 cm) of

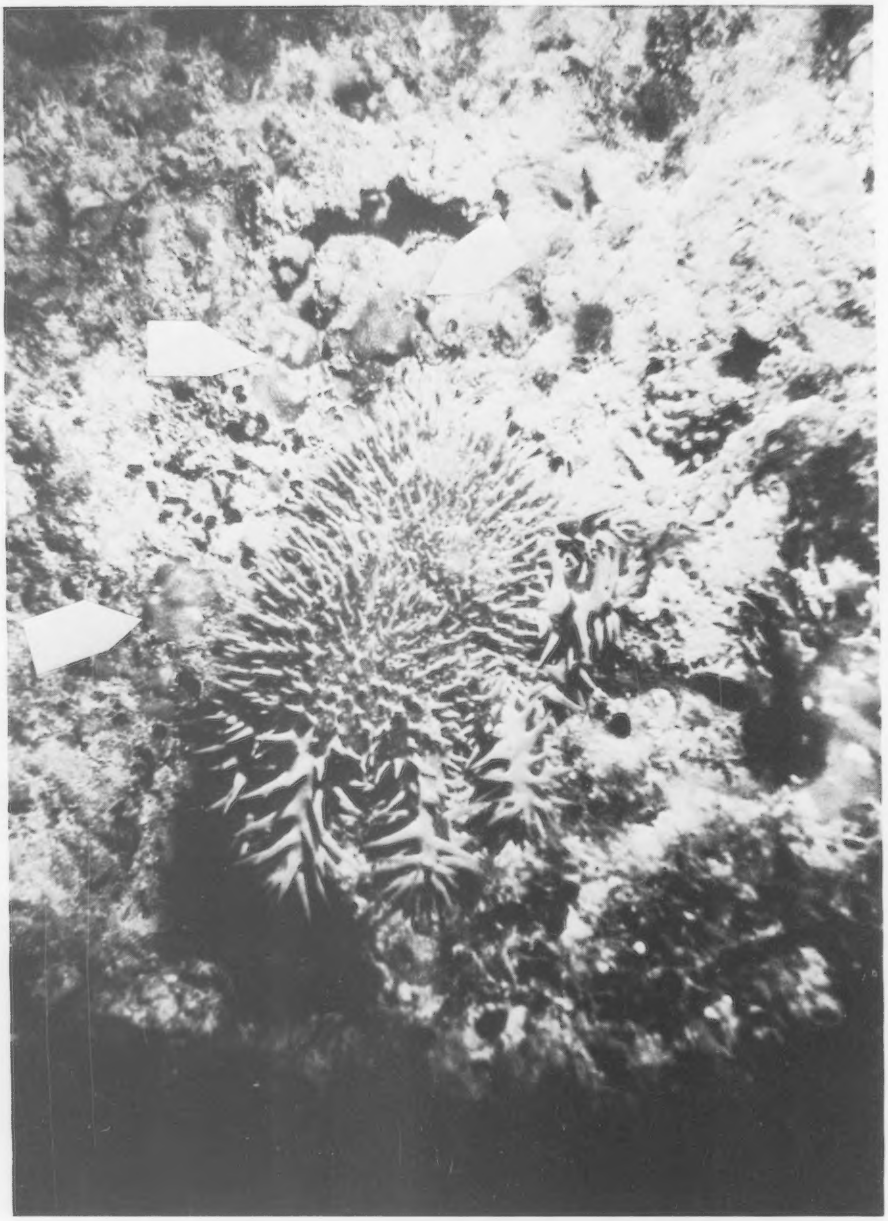

FIGURE 4.—A. *Acanthaster ellisii* in feeding posture on the cliff wall at the Pink Cliff study area. Several of the numerous small *Porites californica* encrustations are indicated by the arrows. The two small coralla in the upper left show damage more characteristic of fishes than of *Acanthaster*. B. The same specimen pulled back to expose the *Porites* nodule (indicated by the arrow) on which it was feeding.

TABLE 3.—Tagging experiment, Pink Cliff station, Isla Partida, March 1971. Behavior, prey, and distances moved between observations.[1]

Specimen	0830-1130 Original location	27 March 1971								28 March 1971						29 March 1971		Total	
		Move	*1* 1415 - 1515	Move	*2* 1615 - 1645	Move	*3* 1930 - 2030	Move	*4* 0920 - 1015	Move	*5* 1115 - 1145	Move	*6* 1430 - 1510	Move	*7* 2030 - 2130	Move	*8* 0915 - 1000	Time	Dist.
		(m)		(m)		(m)		(m)		(m)		(m)		(m)		(m)		(h)	(m)
1	Rock pile	0.6	F/?	0	F/P	0	F/P	—	—	—	—	—	—	—	—	—	—	12	0.6
2	Rock pile	3.7	F/P	0	F/P	0.5	R	1.3	F/P	0	F/P	0.7	T	—	—	—	—	29	6.2
3	Coral gardens	1.4	F/P	0.2	F/P	2.2	R	2.2	F/P	1.7	F/A	0.5	R	0.8	R	3.0	F/P	48	12.0
4	Coral gardens	3.6	F/P	2.6	F/P	0	F/P	—	—	—	—	—	—	—	—	—	—	12	6.2
5	Platform	6.6	i /P	0.5	F/?	1.9	F/P	2.9	F/P	4.5	T	(*I*)	(*I*)	6.0	R	2.2	R	48	24.0
6	Platform	0	F/PP	4.9	R	1.8	R	4.2	F/PP	0	F/PP	1.7	T	6.0	R	6.0	T	48	24.6
7	Cliff base	1.9	R	1.3	T	4.2	F/?	2.7	F/P	0	F/P	7.0	F/P	2.0	F/P	3.0	F/P	48	22.1
8	Coral gardens	2.5	F/Pc	1.0	F/P	(*I*)	(*I*)	1.0	T	2.2	R	2.4	R	1.3	F/PA	1.3	F/Pc	48	11.7
9	Reef rock	(2)			F/P	2.0	F/?	3.0	F/P	0	F/P	4.6	F/A	(*I*)	(*I*)	6.0	F/P	42	15.6
																		330	123.0

[1] F = feeding
? = undetermined
P = *Porites*
— = lost
R = resting
T = traveling
A = coralline algae
(*I*) = missed
Pc = *Pocillopora*

[2] Not tagged until Period 2.

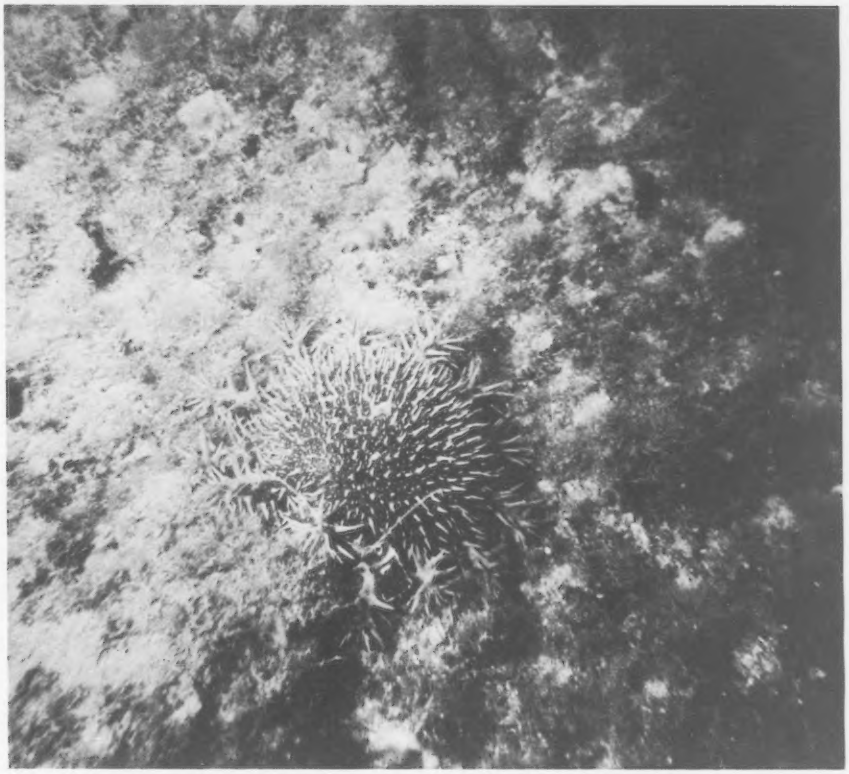

FIGURE 5.—*Acanthaster ellisii*, specimen no. 1, photographed while moving over a large rock in the Pink Cliff study area. The tag is tied to the proximal part of the arm nearest the camera.

plastic PVC (polyvinyl chloride) pipe weighted with lead strips to stand vertically. Small surface buoys equipped with life-jacket lights were anchored near each location to aid in night operations.

Observation and search periods are given in Table 3. Time on the bottom was dependent on our scuba air supply. The greatest care was taken to minimize disturbance of the animals. Specimens on the move were not touched and, to prevent interruption of their activity by stimulating the "shadow reflex" (Hyman, 1955), we tried to avoid swimming over them. The activity of animals at rest was investigated by gently lifting a part of the body with a knife blade. Distance of movement was measured with a meter stick; direction was determined by compass bearings. Following each observation, the pipes and buoy anchors were transferred to the new position.

Specimens in the open were recovered with relative ease; locating them on the rock pile or in its interstices was difficult or even impossible, especially at night. During the course of the study, we failed to recover individuals on six occasions. Three times the "lost" specimen was found on the succeeding search; we suspect that no. 1 and 2 specimens, which were last seen close to their original position (see Figure 2), had moved out of the search area.

Behavior

Table 3 summarizes the 56 observations made during the 48 h of the Pink Cliff study. In 38 instances (68%), the specimen was feeding, that is, it was immobile, hunched or puffed up (Figure 4a), with stomach everted and covering the prey. Feeding was observed in 31 of the 43 daytime observations (72%) and 7 of the 13 night observations (54%). On 12 occasions, 6 at night and 6 during the day, the asteroids were "resting," i.e., they were immobile and the stomach was within the gastric cavity. Six times the observed specimen was "traveling," moving over the substrate on tube feet, one slightly lifted arm leading (Figure 5). Traveling was only observed during the day, but the evidence is insufficient for postulating a diurnal rhythm.

Feeding

Analysis of the 38 feeding observations indicates a definite prey preference. *Porites* comprised 79% of the food (29 observations, plus one of simultaneous feeding on *Porites* and coralline algae). *Pocillopora* was fed on two times (5%) and coralline algae two times (5%). On four occasions (11%) it was impossible to determine the prey.

Specimen no. 8, which fed simultaneously on coral and alga, was also the sole predator on *Pocillopora*. Unusual behavior was also exhibited by no. 6 which, on three occasions, displayed the singular habit of feeding on two or three *Porites* colonies at once.

Movement

The sequence of behaviors observed suggests a general pattern of movement. The individual remains for one or more hours over a small *Porites* encrustation, and then moves off, usually to another corallum which may be several meters distant. A series of feeding stops is followed by a resting period, which may also last for several hours, or by several rest stops interspersed with short moves. It should be noted that, even though specimen no. 3, 5, 6, and 8 were at rest in consecutive observations separated by intervals of 3-13 h, in each case the individual had moved between the observation periods.

The specimen which reacted abnormally to the 1970 tagging operation provides some evidence for the rate at which *A. ellisii* is capable of moving: when returned to the substrate, it immediately embarked on a continuous journey, covering a distance of approximately 10 m in a little over an hour. More refined observations are necessary for estimation of rate of movement, but a rough idea can perhaps be gained from the Pink Cliff study. Dividing the total elapsed time between midpoints of the first and last observation periods (33 h) by the summed distances moved (123 m) gives an average ground coverage of 0.373 m/h. A higher figure is derived from considering the two cases (between period 2-3 and 5-6) in which the intervening intervals were approximately equal (about 3½ h), Distances covered between those periods ranged from 0 to 7.0 m and averaged 2.1 m, giving a rate of 0.6 m/h. Furthermore, average rate in the rock pile and coral gardens, where coral are most abundant, was 0.246 m/h, approximately half of that on the relatively coral-poor platform (0.464 m/h), suggesting correlation with density of the corals.

ACANTHASTER ELLISII AS PREDATOR

Crucial to an evaluation of *A. ellisii* as a potentially destructive coral predator is its foraging behavior throughout its range. North of the island complex, small crustose colonies of *Porites* are the only positively identified prey of *A. ellisii*. In the island complex, which falls in the middle of its known range, *Porites* apparently remains the major food item, with gorgonians, algae, and *Pocillopora* attaining minor importance. (It might be mentioned here that feeding by *A. ellisii* on *Pocillopora* was inferred, rather than actually observed, by Dana and Wolfson (1970).) The few observations which have been made farther to the south suggest that *Pocillopora* is more frequently fed on than *Porites*.

This apparent shift in prey preference may

reflect the distribution of corals in the Gulf of California. From an ecological standpoint, the ranges for coral genera given in the most recent treatment of the subject (Squires, 1959) can be misleading. For example, Squires shows the northern limit for extant *Pocillopora* species as a line extending across the Gulf from about the level of Santa Rosalía to Guaymas. The line is based on a single specimen of *Pocillopora robusta* (= *elegans*) collected by an Allan Hancock Expedition at Isla San Marcos (Durham and Barnard, 1952). John Garth of the Hancock Foundation informs us that the specimen was dredged in 20 fathoms south of Isla San Marcos (lat. 27°09′05″N; long. 112°04′25″W) and appears to have been taken alive. In our experience, the only common coral north of the island complex is *Porites*, and this Isla San Marcos specimen must represent an isolated outpost of *Pocillopora*. Squires' Table 1, summarizing the diminution of the hermatypic coral fauna in the northern regions of the Gulf, gives a more accurate picture of the situation as we have seen it. It seems obvious, then, that if *A. ellisii* is primarily an obligate coral feeder, its major prey through the northern part of its range must be *Porites*.

The varying growth forms of the corals may also enter into the prey preference of *A. ellisii*. In gross morphology, *Porites* is highly plastic, showing phenotypic gradation from encrusting colonies in the northern part of its range to columnar, branched, or nodular forms in the south. However, the influence of latitude is cancelled in protected situations in the lower mid-Gulf, such as Bahía Coyote and the inner bay at Puerto Escondido, and *Porites* tends to assume the dome-shaped heads and large nodular form typical of the southern type. We have never seen *A. ellisii* in these quiet-water environments.

It is noteworthy that we have never seen *A. ellisii* on large or ramose corals at any locality. The *Porites* being preyed on in all of our observations were so small that the sea stars appeared to be sitting on a coral-free substrate; only when the animal was lifted could the coral be seen and identified. Furthermore, our observations of predation on *Pocillopora* all involved feeding at substrate level. In a crude field trial, a traveling specimen immediately began to feed on a broken branch that we had placed in its path; and the three observations at Pink Cliff station (all by specimen no. 8) involved one instance of feeding on the underside of a low branch and two on broken branches. However, at the end of the study, no. 8 fed on a ramose *Pocillopora* when dropped directly on top of it, and Faulkner (pers. comm.) reports that south of La Paz, where *Pocillopora* assumes a densely packed, reeflike formation, *A. ellisii* feeds on top of the colonies. It thus appears that some factor or factors may prevent the asteroid from mounting upright, solitary corals.

Weber and Woodhead (1970) reported that fish and crabs living among the branches of *Stylopora*, a close relative of *Pocillopora*, defend that coral from attack by *A. planci*. *Pocillopora's* symbionts (Figure 3) perhaps serve a similar function.

The experimental work of Barnes, Brauer, and Jordan (1970) and Brauer, Jordan, and Barnes (1970) may explain the marked preference of *A. ellisii* for discrete, low coralla. Working with *A. planci*, these investigators demonstrated that, while the tube feet are sensitive to nematocysts, the stomachs respond positively to nematocyst-containing tissue. From these experiments, and from the observation that the sea star uses its arms and spines as much as possible when climbing coral heads, they infer that the humped feeding position of *A. planci* may serve to keep the tube feet free of the prey's stinging polyps. If *A. ellisii* responds to nematocysts in the same ways, small, isolated, crustose coralla that can be easily straddled and then covered by the stomach would constitute more acceptable prey and would be selected over larger growths.

Examination of small *Porites* fed upon by *A. ellisii* suggests that the entire colony is not necessarily destroyed; white patches, which indicate that the zooxanthellae have been digested, are left mainly on regions that protrude above the general level of the substrate. We consistently observed, however, that the entire corallum appears to be covered with a mucous film, and suggest that the extent of the damage inflicted on small *Porites* by *A. ellisii* bears further investigation.

It should be borne in mind that not all coral damage can be attributed to *A. ellisii*. The report of predation by *Pharia pyramidata* (Dana and Wolfson, 1970) is the first indication that the smaller asteroid, which occurs throughout the coral areas of the Gulf, is also a coral-feeder. And, of course, certain fishes are well known to be coral-browsers and commonly leave gouge marks on the coralla.

The amount of *Porites* available to *A. ellisii* in the preferred small form is difficult to evaluate. The vast numbers of small encrustations have, perhaps, been unappreciated by coral workers in the Gulf. Dana and Wolfson (1970) estimate approximately 3% coral coverage in their survey areas. While our attempt to count the numbers of *Porites* at Pink Cliff station does not warrant critical treatment, we estimated that the encrustations covered roughly 10% of the substrate.

The important question of how much coral is necessary to maintain the *A. ellisii* population in the Gulf of California must await some definitive information on coral growth rates in that physical regime. Dana and Wolfson (1970) calculated that an average-sized specimen would consume 5.3 m^2 of coral per year. Our rough estimate of 10% coral coverage at Pink Cliff station would provide 20 m^2 of *Porites* per individual. If that can be extrapolated to the Gulf as a whole, even with an allowance for competition, it would appear that *A. ellisii* is living well within the available resources of its environment.

Miscellaneous Observations

In its natural environment, *A. ellisii* reacts to a touch or a cast shadow with a rapid retraction of the dermal papulae, resulting in an overall color change from dark red (or orange or yellow) to dull gray. If not further disturbed, the papulae are soon extruded, restoring the original color; if removed from the water, however, the gray persists. This habit reconciles the conflicting descriptions of the species as gray (Steinbeck and Ricketts, 1941) and as rufous (Ziesenhenne, 1937). Madsen (1955) mentions the same phenomenon for *A. planci*.

When feeding or at rest, the aboral spines are partly hidden in the papulae, and *A. ellisii* presents a deceptively harmless appearance. Although it can be more easily removed from the substrate than most asteroids, it should be handled with caution. Ziesenhenne (1937) was uncertain of the toxicity of the spines, but two of us (Barham and Wolfson) can attest to the painful and long-lasting effects of a puncture.

To augment the meager morphological data available for *A. ellisii*, we collected and measured six specimens at the termination of the 1971 study. Number of arms varied from 12 to 15, madreporic bodies from 5 to 9. Overall diameters ranged from 10.7 to 15.4 cm, disk diameters from 7.6 to 9.1 cm. Ratios of disk diameter to arm length (calculated from overall diameter minus disk diameter) ranged from 1.3 to 1.6.

(In comparing specimens, it should be noted that their general appearance will differ markedly, depending on the method of preservation. Dried specimens tend to "collapse" and appear less spiny, much flatter, and more bat-armed than if either fixed in preservative before drying or maintained in the preservative. Our specimens were preserved in Formalin[3] and then dried.)

Distribution of *Acanthaster* adjacent to the Gulf of California

We have found no *Acanthaster* at Banderas Bay, our most southerly station, although the environment seems ideal for the sea star. Specimens designated as *A. ellisii* have been reported at Clarión, Roca Partida, and Socorro Islands in the Revillagigedo Group, some 24° south of the tip of Baja California (Ziesenhenne, 1937), and the subspecies, *A. ellisii pseudoplanci*, was described (Caso, 1962) from specimens collected at various locations in those islands. Whether these identifications will survive taxonomic review of the genus remains, of course, to be seen.

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

It would be of considerable interest to know if *Acanthaster* is present on the Tres Marías Islands and along the great stretch between Farallon, San Ignacio, and Panamá, or if the distribution of the genus is indeed as discontinuous as it now appears.

CONCLUSION

Our adherence to the taxon, *Acanthaster ellisii*, stems from the conviction that the binomen is valid for the Gulf of California. Regardless of final decisions on the taxonomy of the more southerly, oceanic populations of *Acanthaster*, we believe that the Gulf populations constitute a distinct form.

Dana and Wolfson (1970), who have observed both *A. planci* and *A. ellisii* in the field, point out that the behavior of the two species is strikingly different. The information presented here indicates that, unlike *A. planci*, *A. ellisii* is not cryptic during daylight hours and feeds both night and day. Even where its population densities are similar to those given by Chesher (1969) for infestation levels of *A. planci*, *A. ellisii* does not appear to aggregate or to migrate as a population.

In gross morphology, *A. ellisii* also appears to be quite distinct from *A. planci*. Madsen (1955) stresses the disk-diameter to arm-length ratio as the most conspicuous difference between the American and Indo-West Pacific forms; our ratios fall well below the 1.9:2.2 ratio established for *A. planci*. (Other taxonomic characteristics appear to be too subtle and variable for comment by a nonspecialist.)

In conclusion, from the evidence presented in this paper, *A. ellisii* gives every appearance of living in harmony with its environment. There is nothing to suggest that it represents a threat to the coral fauna within its geographic range or a potential threat to any area beyond it.

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SOME METAZOAN PARASITES OF THE EASTERN PACIFIC SAURY, *COLOLABIS SAIRA*

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ABSTRACT

Parasite composition of the eastern Pacific saury, *Cololabis saira*, and severity of infections were investigated to determine their possible effects on potential food fish markets and to assist in determining population structure of the stock. Infection data from two copepods and one acanthocephalan are presented and examined for host dependent factors, temporal and spacial variation, and variation between saury with different scale features (hypothesized spring- and autumn-born fish). The acanthocephalan infecting saury was also identified in the steelhead trout, *Salmo gairdneri*, which is reported as a second definitive host. It is concluded that because of parasites, only 30 to 60% of marketable-sized saury occurring off the Washington-Oregon coast would be acceptable as fresh-food fish sold in the round although most would be acceptable as canned products. The parasite data do not indicate that fish with the two different patterns of growth on the scales are independent subpopulations.

The eastern Pacific saury, *Cololabis saira*, is a pelagic teleost occurring in offshore waters along the Pacific coast of North America. Although previously recognized mainly as a food source for albacore, *Thunnus alalunga*, the saury resource in the eastern Pacific attracted the interest of foreign and domestic fishermen during the late 1960's. Potential domestic markets included fresh, frozen, and canned products for human consumption. Studies to determine the parasite composition and severity of infections, believed an important consideration in assessing the potential value of saury as a food fish, were undertaken by the National Marine Fisheries Service at the Northwest Fisheries Center. Parasite data were also examined for their possible use in determining the population structure of saury in the sampled area. Preliminary growth and scale studies (Hughes, in press; Mosher[2]) suggested two spawning groups of saury, spring- and autumn-born.

Initial samples collected off California in 1969 and limited information from two previous reports (Eberhardt, 1954; Sokolovskii, 1969) indicated that the eastern Pacific saury were primarily parasitized by two species of copepods and one acanthocephalan. Results of a detailed study by Baeva (1970) indicated the eastern Pacific saury are infected by at least 10 species of parasites. Eberhardt reported the copepod *Pennella* sp. parasitized more than 20% of 250 saury captured off California in 1950-52. Although several *Pennella* species infecting marine fish have been described and partial life histories determined, detailed work on the saury parasite appears lacking. My preliminary studies and a recent Soviet study by Sokolovskii indicated that up to 90% of the eastern Pacific saury were infested by the copepod *Caligus macarovi* Gussev. This copepod also infects the western Pacific saury, but Sokolovskii and Baeva reported that *Pennella* sp. is peculiar to the eastern Pacific stock. The acanthocephalan detected in the preliminary studies was described by Laurs and McCauley (1964) as a new species, *Rhadinorhynchus cololabis*. Further reports on this species also appear lacking.

This report presents data on the numbers and incidence of infestation for *Pennella* sp., *Caligus*

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[2] Mosher, K. H. Age determination procedures for saury (*Cololabis saira*) from the northeastern Pacific Ocean, using scales. Manuscr. in preparation. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash.

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macarovi, and *Rhadinorhynchus cololabis* infections found on and in Pacific saury captured off the Oregon, Washington, and British Columbia coasts during August-September 1970-71. Incidence of infestation and numbers of scars resulting from previous copepod infestations are presented by geographical areas and correlated to size, age, and possible racial composition of the host species. Sex ratio and length data are included for *R. cololabis* recovered from saury; a second definitive host infected by this acanthocephalan is reported.

MATERIALS AND METHODS

A total of 4,396 saury sampled from 13 individual fish schools captured in offshore waters along the Pacific coast of North America between lat. 44°01'N and lat. 49°16'N were involved in this study. Fish were captured with a modified purse seine-artificial light attraction system (Ellis and Hughes, 1971). Random samples were collected and frozen for processing at shoreside facilities. In the laboratory, fish samples were examined for copepod parasites and scars from previous copepod infestations. Simultaneously, host length, weight, sex, maturity, and age indicators were collected. Digestive tracts from 20 saury randomly subsampled from 12 of the 13 samples were placed in 10% Formalin[3] and later examined for metazoan parasites with the aid of a dissecting microscope (7× – 50×). Each *R. cololabis* was measured (trunk length) to the nearest 0.5 mm, and its sex determined by dissection and examination of the posterior portion. Females were generally swollen with bipolar eggs, and the uterus was easily distinguished from cement glands in the males. Host age was determined from scales. Patterns of growth displayed on the scales were used to identify the two hypothesized spawning groups, spring- and autumn-born fish.

Specimens were photographed in a circumilluminated lightbox, using standard techniques and materials.

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Two copepods, *Pennella* sp. and *Caligus macarovi*, and the acanthocephalan *Rhadinorhynchus cololabis* made up the major macroparasitic fauna of the eastern Pacific saury. Other than an occasional nematode located in the body cavity, additional metazoan parasites were not detected.

Incidence and intensity of infection of parasites recovered on and in saury throughout the study are presented by sample in Table 1.

Pennela sp.

An adult fish heavily parasitized by this large copepod is shown in Figure 1. In addition to three mature females (one with broken egg strings), two juveniles are shown — one posterior to the pectoral fin and the other posterior to the pelvic fin and above the anal finlets. Figure 2 shows an entire mature female (A), with a juvenile (B), after removal from the host. The external portion of this parasite usually protruded from the host at some point below the darkly colored dorsal surface but above the lateral line; and the head was usually lodged in or adjacent to the host's heart or major blood vessels. The tissue invading portion ends where the trunk diameter increases notably. Infected hosts weighed as much as 17% less than uninfected hosts of equal length, and extensive destruction of host tissue occurred during degeneration of the parasite.

Pennella sp. was frequently encountered in each of the six samples collected in 1970 but was detected in only one of seven samples collected in 1971. Incidence of infection for schools sampled in 1970 ranged from 17.0 to 21.6% (mean 18.4%) off Oregon and 11.5 to 18.4% (mean 14.5%) off Washington. Multiple infections were common. Only 2.1% of one school was infected in 1971 and no multiple infections were detected.

The 1970 data showed a trend toward increasing incidence of infection with increasing host size. To determine whether this noted increase was a function of increasing host age, length, or both, Washington and Oregon *Pennella* sp. data were analyzed by host age groups, length

TABLE 1.—Parasites recovered from Pacific saury, *Cololabis saira*, captured off the Oregon and Washington coasts in 1970 and the Oregon and Washington-southern British Columbia coasts in 1971.

Year and coastal area	Location		No. of fish examined	*Pennella* sp.				*Caligus macarovi*				*Rhadinorhynchus cololabis*			
	Lat. N.	Long. W		Total no.	No. per infected fish: Range	No. per infected fish: Mean	Incidence of infection (%)	Total no.	No. per infected fish: Range	No. per infected fish: Mean	Incidence of infection (%)	Total no.	No. per infected fish: Range	No. per infected fish: Mean	Incidence of infection (%)
1970:															
Oregon	45°03′	125°50′	300	93	1-6	1.82	17.0	21	1-2	1.10	6.3	—	—	—	—
			20	—	—	—	—	—	—	—	—	98	1-14	7.0	70.0
	44°33′	125°11′	300	96	1-5	1.48	21.6	57	1-2	1.19	16.0	—	—	—	—
			20	—	—	—	—	—	—	—	—	74	1-20	4.1	90.0
	44°30′	125°08′	300	94	1-4	1.74	18.0	61	1-4	1.15	17.7	—	—	—	—
			19	—	—	—	—	—	—	—	—	47	1-13	3.4	73.9
Washington	47°43′	126°02′	284	47	1-5	1.20	13.7	158	1-5	1.44	38.7	—	—	—	—
			20	—	—	—	—	—	—	—	—	16	1-4	2.0	40.0
	47°41′	125°58′	191	25	1-4	1.14	11.5	81	1-4	1.36	42.4	—	—	—	—
			20	—	—	—	—	—	—	—	—	20	1-4	1.8	55.0
	47°39′	126°00′	192	44	1-3	1.26	18.4	62	1-5	1.35	24.0	—	—	—	—
			20	—	—	—	—	—	—	—	—	27	1-9	2.7	50.0
1971:															
Oregon	44°01′	125°01′	419	0	—	0	0	20	1-2	1.11	4.3	—	—	—	—
			20	—	—	—	—	—	—	—	—	1	1	1.0	5.0
	43°55′	124°59′	508	0	—	0	0	34	1	1.00	6.7	—	—	—	—
			20	—	—	—	—	—	—	—	—	0	—	0	0
	43°54′	125°00′	508	0	—	0	0	37	1	1.00	7.3	—	—	—	—
			20	—	—	—	—	—	—	—	—	2	1	1.0	10.0
	44°02′	125°02′	268	0	—	0	0	18	1-2	1.06	6.3	—	—	—	—
			20	—	—	—	—	—	—	—	—	4	1-2	1.3	15.0
	43°58′	125°04′	507	0	—	0	0	14	1	1.00	2.8	—	—	—	—
Washington-British Columbia	48°21′	126°04′	513	11	1	1.00	2.1	41	1-2	1.03	7.8	—	—	—	—
			19	—	—	—	—	—	—	—	—	109	1-13	6.4	89.5
	49°16′	127°06′	106	0	—	0	0	24	1-3	1.26	17.9	—	—	—	—
			20	—	—	—	—	—	—	—	—	21	1-5	2.3	45.0
Total			4,396	410				628				419			

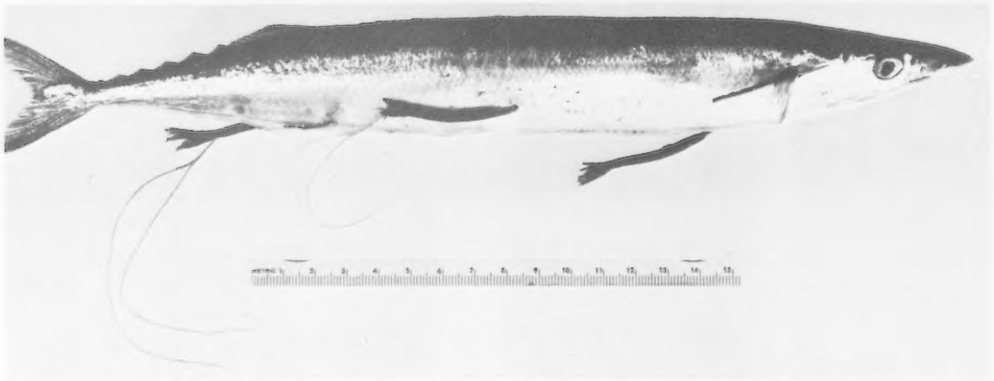

FIGURE 1.—Pacific saury with three adult female and two juvenile copepods, *Pennella* sp. Oken.

groups, and length groups within age. The increasing incidence of infection was found to be a function of age (Table 2) but not length. A chi-square test was employed to test the null hypothesis that the occurrence of infected II-, III-, and IV-year-old-fish was the same in potential harvest areas off Washington and Oregon (0.05 level). This hypothesis was rejected (0.025 level) for II-year-olds and accepted for III- and IV-year-olds.

Caligus macarovi

Incidence of infection by *C. macarovi* (Figure 3) showed both annual and geographic variability (Table 1). The proportion of infected saury in 1970 samples ranged between 6.3 and 17.7% (mean 12.8%) off Oregon and between 24.0 and 42.4% (mean 35.0%) off Washington. Infections were less common in 1971 samples, 2.8 to 7.3% (mean 5.5%) off Oregon and 7.8 to 17.9% (mean 12.9%) off Washington. These percentages, however, are certainly minimum estimates of the rate of infection of the sampled population because some *C. macarovi* dropped off captured fish.

Both 1970 and 1971 Washington and Oregon data were separately examined for changes in infection rate with increasing host size and age. No trends of change related to those factors

TABLE 2.—Numbers and percent incidence of *Pennella*-infected saury in different host age groups in samples taken in September 1970 from off the Washington and Oregon coasts.

Fishing area and type of data	Host age (years)					
	I	II	III	IV	V	VI
Washington coast:						
No. fish examined	9	326	244	22	4	1
No. fish infected by *Pennella* sp.	0	55	98	7	2	1
Incidence of infection (%)	0	16.87	40.16	31.81	50.00	100
Oregon coast:						
No. fish examined	314	322	70	10	—	—
No. fish infected by *Pennella* sp.	26	80	32	5	—	—
Incidence of infection (%)	8.26	24.84	45.71	50.00	—	—

FIGURE 2.—Mature female *Pennella* sp. (A), with a juvenile (B), after removal from the host.

were detected. Accordingly, fish from individual schools captured in each area and year were combined and tested by chi-square analysis between areas. In both 1970 and 1971, numbers of fish infected with *C. macarovi* were significantly higher (0.05 level) off Washington than off Oregon.

This ectoparasitic copepod usually occurred more frequently than *Pennella* sp., but was considered less burdensome due to small size,

method of infection, and minimal host-tissue damage (Figure 3). Hotta (1962) reports that tissue damaged by *C. macarovi* infestation is limited to the epidermis and mucosa while the muscle is not penetrated.

Scars from Previous Copepod Infections

Pacific saury were heavily scarred from previous infections by *Pennella* sp. and *C. macarovi*. In many cases the scar's shape clearly indicated a previous *C. macarovi* infection, but most old scars could not readily be discerned between specific causes (Figure 4). Accordingly, all scars were treated equally.

The percentage of scarred fish and the average number of scars per fish generally increased as a function of increasing age. This is shown in Table 3 where numbers and percentages of scarred fish are categorized by age into three

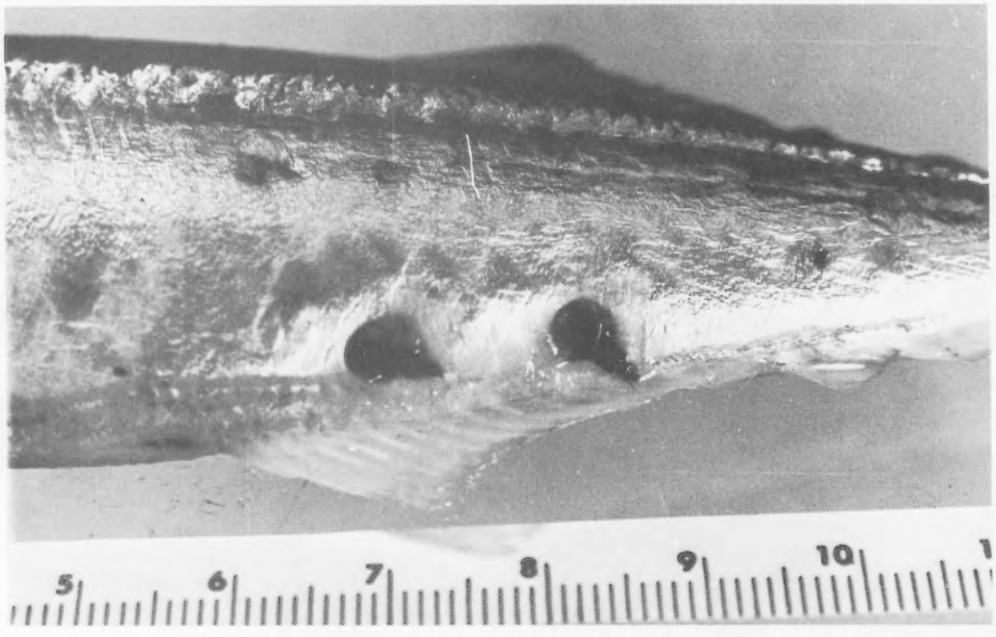

FIGURE 3.—Pacific saury infected by the copepod, *Caligus macarovi* Gussev.

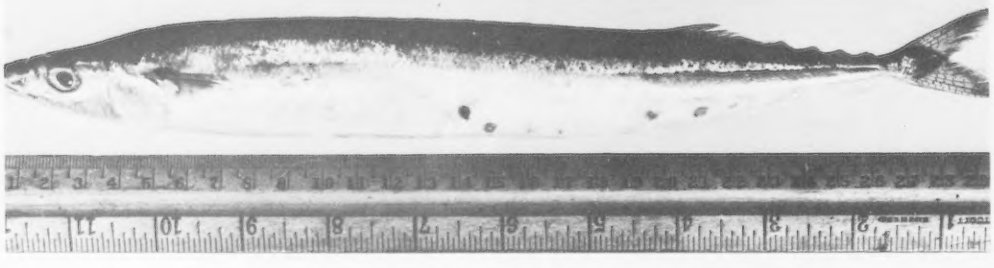

FIGURE 4.—Examples of scars resulting from previous infections by copepods on Pacific saury.

TABLE 3.—Pacific saury scarred from infections with the copepods *Pennella* sp. and *Caligus macarovi* as sampled off the Pacific coast of North America during August-September 1970-71.

Year and coastal area	Fish age (years)	No. fish examined	Fish with 1-3 scars		Fish with >3 scars		Total scarred fish	
			No.	%	No.	%	No.	%
1970:								
Oregon	I	314	224	71.3	20	6.4	244	77.7
	II	320	232	72.5	40	12.5	272	85.0
	III	70	47	67.1	15	21.4	62	88.5
	IV	10	5	50.0	5	50.0	10	100
Washington	I	9	5	55.6	4	44.4	9	100
	II	326	150	46.0	163	50.0	313	96.0
	III	244	68	27.9	196	80.3	237	97.2
	IV	22	5	22.7	17	77.2	22	100
1971:								
Oregon	I	576	172	29.9	1	0.2	173	30.1
	II	729	356	48.8	7	1.0	363	49.8
	III	137	79	57.7	3	2.2	82	59.9
Washington-southern British Columbia	II	26	13	50.0	2	7.7	15	57.7
	III	104	62	59.6	8	7.7	70	67.3
	IV	277	157	56.7	26	9.4	183	66.1
	V	97	54	55.7	7	7.2	61	62.9

groups—those fish with one to three scars, those with more than three scars, and total number of scarred fish. In 1970 when scarred fish were more prevalent (77.7-100%), the percentage of fish with one to three scars decreased with increasing age whereas those with more than three scars increased. The fact that 1971 fish were less severely scarred than 1970 fish is puzzling.

Rhadinorhynchus cololabis

This acanthocephalan was associated primarily with the lower digestive tract although worms were also found attached in the midstomach area (Figure 5). Tissue damage around the point of attachment appeared minimal, and the worm's proboscis rarely protruded through the wall of the digestive tract. Female *R. colo-*

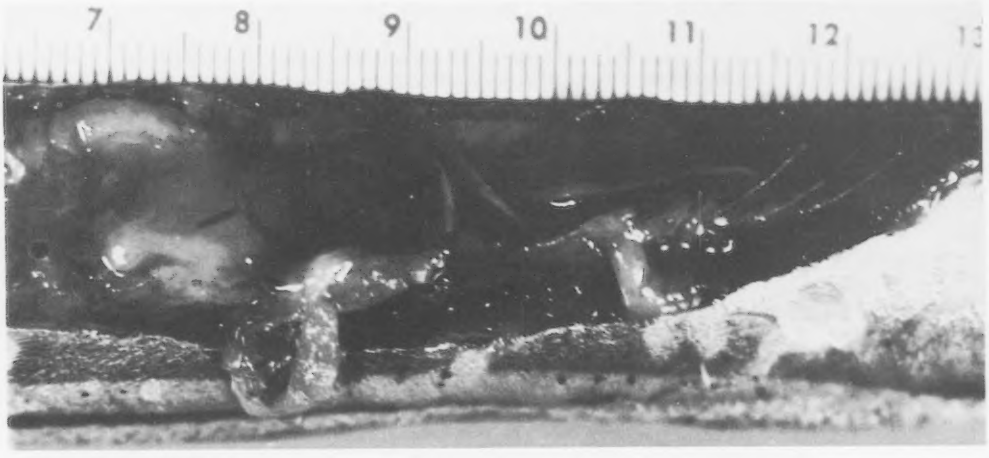

FIGURE 5.—Lower digestive tract of a Pacific saury typically infected by the acanthocephalan, *Rhadinorhynchus cololabis* Laurs and McCauley.

labis were much larger than males and occurred less frequently (Table 4). The range of trunk lengths for both males and females is increased from the original reporting—females 18.0 to 26.7 mm, now 13.5 to 35.0 mm, and males 9.20 to 12.16 mm, now 7.5 to 14.0 mm. All females with trunk lengths exceeding 15.0 mm were swollen with bipolar eggs.

Occurrence of this parasite as presented in Tables 1 and 4 was minimal since worms were often squeezed from the host's anus as fish were brailed aboard the ship. Occurrence of *R. cololabis* showed inconsistent geographic and annual variability precluding further meaningful analysis. Proportions of infected saury in 1970 samples ranged between 70.0 and 90.0% (mean 78.0%) off Oregon and between 40.0 and 55.0% (mean 48.3%) off Washington. Like the parasitic copepods, incidence of infection was generally lower in 1971, ranging between 0 and 15.0% (mean 7.5%) off Oregon and between 45.0 and 89.5% (mean 67.2%) off Washington. Rates of infection were found to be independent of host size and age.

R. cololabis in Steelhead Trout

The steelhead trout was found bearing the adult form of the same acanthocephalan identified in Pacific saury. Steelhead trout had previously been reported with an acanthocephalan identified as *Rhadinorhynchus* sp., Shaw (1947); however, more recent or specific reports have not been located.

C. M. Senger, Professor of Biology, Western Washington State College, Bellingham, Wash., recovered two Acanthocephala from steelhead trout captured in Skagit County, Wash., in 1967-68. He later compared these with specimens I supplied from Pacific saury and concluded both hosts carried *R. cololabis*. Additional steelhead trout from Skagit County (1969-72) and from high-seas areas of the northwestern Gulf of Alaska (August 1970) were subsequently examined. Nine of 28 steelhead trout from Skagit County and 4 of 22 steelhead trout from the northwestern Gulf of Alaska were infected with *R. cololabis*. Multiple but not severe infections were noted from hosts collected in both areas. The heavy egg load carried by female *R. cololabis* indicated the steelhead trout to be a second definitive host.

Copepod Infections in Two Possible Subpopulations of Saury

Chi-square analysis was applied to test the null hypothesis that no significant differences (0.05 level) in numbers of infected fish existed between the two possible subpopulations (spring- and autumn-born saury) that were classified by means of scale features. The two indicators

TABLE 4.—Intensity of infection, sex ratio, and trunk length of *Rhadinorhynchus cololabis* from Pacific saury captured off the Pacific coast of North America during August-September 1970-71.

Year and coastal area	Location		No. fish examined	Incidence of infection (%)	Sex ratio (%)		Trunk length (mm)			
							Males		Females	
	Lat. N	Long. W			M	F	Range	Mean	Range	Mean
1970:										
Oregon:	45°03′	125°50′	20	70.0	64.3	35.7	8.0-13.0	10.1	16.0-27.0	21.0
	44°33′	125°11′	20	90.0	77.0	23.0	7.5-12.0	9.4	16.0-32.0	23.0
	44°30′	125°08′	19	73.9	66.0	34.0	8.5-13.0	10.4	17.5-28.0	21.5
Washington	47°43′	126°02′	20	40.0	81.2	18.8	8.5-12.0	10.1	22.0-23.0	22.5
	47°41′	125°58′	20	55.0	55.0	45.0	9.5-12.0	10.6	13.5-27.5	22.8
	47°39′	126°00′	20	50.0	63.3	36.7	8.5-12.5	10.5	15.0-33.0	22.8
1971:										
Oregon	44°01′	125°01′	20	5.0	100.0	—	12.0-	12.0	—	—
	43°55′	124°59′	20	0	—	—	—	—	—	—
	43°54′	125°00′	20	10.0	50.0	50.0	10.0-	10.0	17.0-	17.0
	44°02′	125°02′	20	15.0	75.0	25.0	10.0-14.0	12.0	21.0-	21.0
Washington-southern British Columbia	48°21′	126°04′	19	89.5	69.3	29.7	10.0-13.0	11.0	15.0-35.0	23.8
	49°16′	127°06′	20	45.0	81.0	19.0	10.0-14.0	11.5	16.0-26.0	20.3

were *Pennella* sp. and *C. macarovi* since insufficient data excluded use of the acanthocephalan.

As previously shown, infections by *Pennella* sp. increased with increasing host age, and *C. macarovi* infections were found to be independent of host age or length. Accordingly, chi-square tests of *Pennella* sp. infections were conducted for spring-born versus autumn-born fish by individual age groups for each area during 1970. *C. macarovi* infections were compared after combining all host age groups within each area for 1970 and 1971.

Results of chi-square tests are summarized in Table 5. The only significant difference in numbers of saury infected by *Pennella* sp. occurred between spring- and autumn-born II-year-olds captured off Oregon in 1970. No significant differences between numbers of spring- and autumn-born saury infected by *C. macarovi* existed in either area during 1970 and 1971.

CONCLUSIONS AND SUMMARY

The eastern Pacific saury was found to be infected with two species of copepods and one acanthocephalan, in addition to being scarred from previous copepod infections. Mean incidence of *Pennella* sp. infections was 18.4% off the Oregon coast and 14.5% off the Washington coast in 1970, but this parasite was rarely found

TABLE 5.—Numbers and percentage incidence of copepods (*Pennella* sp. and *Caligus macarovi*) in two possible subpopulations of eastern Pacific saury. Chi-square values are presented testing the null hypothesis that no significant difference in numbers of infections exists (0.05 level) between the hypothesized spring- and autumn-born fish. Fish ages are in parentheses.

Year and area	Pacific saury examined for *Pennella* sp.	Number of saury			Incidence of infection (%)	χ^2	Null hypothesis	
		Noninfected	Infected	Total			Accept	Reject
1970:								
Washington	Spring born (II)	221	47	268	17.5	1.03	X	—
	Autumn born (II)	51	7	58	12.7			
	Spring born (III)	103	45	148	30.4	0.42	X	—
	Autumn born (III)	63	33	96	34.4			
Oregon	Spring born (II)	154	64	218	29.4	6.93	—	0.01
	Autumn born (II)	86	16	102	15.7			
	Spring born (III)	23	13	36	36.1	2.70	X	—
	Autumn born (III)	15	19	34	55.8			

Year and area	Pacific saury examined for *Caligus macarovi*	Number of saury			Incidence of infection (%)	χ^2	Null hypothesis	
		Noninfected	Infected	Total			Accept	Reject
1970:								
Washington	Spring born	329	114	443	25.7	0.58	X	—
	Autumn born	126	37	163	22.7			
Oregon	Spring born	503	71	574	12.4	1.11	X	—
	Autumn born	118	22	140	15.7			
1971:								
Washington	Spring born	368	32	400	8.0	3.16	X	—
	Autumn born	96	15	111	13.5			
Oregon	Spring born	1,211	83	1,294	6.4	2.42	X	—
	Autumn born	150	16	166	9.6			

in 1971. Incidence of infection increased with host age. Mean incidence of *C. macarovi* infections was 12.8% off Oregon and 35.0% off Washington in 1970 and also decreased in 1971 to 5.5% off Oregon and 12.9% off Washington. Infection rates were independent of host size and age. The incidence of scars resulting from previous copepod infections was very high. Mean incidence of *R. cololabis* in 1970 was 78.0% off Oregon and 48.3% off Washington and decreased substantially during 1971. Infection rates were independent of host size and age. Trunk length measurements increased the known length range for both male and female worms.

R. cololabis was also identified in steelhead trout, which is reported as a second definitive host. It seems most likely that both hosts are infected through a common food organism carrying the acanthor stage although steelhead trout are known to feed on saury in ocean waters.

For aesthetic reasons, presence of copepod parasites or scars, and to a lesser extent the acanthocephalan, would undoubtedly limit usage of saury in the round as a fresh fish product for human consumption. Saury infected by the obnoxious appearing *Pennella* sp. and those with multiple infections of *C. macarovi* or numerous scars, would undoubtedly be rejected by consumers. Although western Pacific saury are not infested by *Pennella* sp., Nishimura (1964) reports that saury heavily blemished by *C. macarovi* have a lower commercial value than nonblemished fish. The acanthocephala are not as unsightly as either copepod, although the bright orange worms are often clearly visible protruding from the anus.

Considering apparent annual and age dependent changes in incidence of infection, only 30 to 60% of the market-sized saury occurring in Washington-Oregon coastal waters appear to be acceptable as a fresh-food fish sold in the round. Although some geographical variations of infection rates and occurrence of scars have been noted, the percentage of fish usable as a fresh product appears nearly equal off Washington and Oregon.

Test packs prepared by the Pacific Fishery Products Technology Center, National Marine Fisheries Service, Seattle, have indicated that these parasites have practically no effect on canned saury products. Acanthocephala are removed with the vicsera, and *C. macarovi* can be scraped free with resulting wounds and old scars presenting no qualitative or aesthetic problems. Uninfected portions of saury with pennellids can also be used.

Pennella sp. and *C. macarovi* were also employed as racial indicators by comparing their occurrence between fish displaying spring- and autumn-born growth patterns on their scales. Seven of eight chi-square tests showed no significant differences (0.05 level), between fish of the two scale features; thus, evidence from the parasite data does not indicate the existence of separate populations. Although use of parasites as biological indicators is not a strong test of population structure, particularly without knowledge of the parasites' life history, biochemical and growth studies likewise do not indicate existence of two genetically isolated populations (Hughes, see footnote 2).

ACKNOWLEDGMENTS

I thank Paul L. Illg, Professor of Zoology, University of Washington, for confirming identification of the copepods, and Clyde M. Senger, Professor of Biology, Western Washington State College, for his cooperative work on the acanthocephalan and review of this manuscript.

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AGE, GROWTH, AND REPRODUCTION OF THE NORTHERN PUFFER, *SPHOEROIDES MACULATUS*[1]

JOANNE L. LAROCHE[2,3] AND JACKSON DAVIS[4]

ABSTRACT

Rings on vertebral centra of the northern puffer, *Sphoeroides maculatus*, were shown to be true year marks. Age groups 0 to V were found in 1,128 specimens collected from Chesapeake Bay. Females were significantly larger than males at each age. Most growth in length took place during the first growing season from June through October. Sexual maturity was reached at age I. Peak spawning occurred in June and July.

The northern puffer, *Sphoeroides maculatus* (Bloch and Schneider), occurs on the Atlantic coast of North America from Newfoundland to Flagler County, Fla. (Shipp and Yerger, 1969). It is the only tetraodontid that is abundant along the middle Atlantic coast and that comprises a large part of the spring and fall commercial catches in Chesapeake Bay. During the period 1962 to 1970, total annual landings from Chesapeake Bay ranged from 1 to 12 million pounds. The steady northward progression of commercial landings in the spring from North Carolina to Chesapeake Bay and the southward progression of catches in the fall suggest an annual coastal migration.

There is little published information on the life history of the northern puffer. Welsh and Breder (1922) reported the food habits, larval development, and weight-length relationships of puffers from New Jersey. Shipp and Yerger (1969) reviewed the taxonomy of *S. maculatus*.

This paper describes a technique for determining the age of the northern puffer and reports the rate of growth, weight-length relationships, age at sexual maturity, and spawning time.

This is the first published report of age determination for a tetraodontid.

MATERIALS AND METHODS

Age and growth determinations were based on 123 fish captured during November 1969 and 1,005 fish collected from April through November 1970 from lower Chesapeake Bay, Mobjack Bay, and the mouths of the York and Rappahannock rivers, Va. A homogeneous puffer population in the area sampled is assumed. Fish were primarily obtained from commercial pound nets and haul seines but also with a push net, beach seine, and trawl and from commercial crab pots.

Total length was measured from the tip of the snout to the center of the flared caudal fin. Fish with a distended ventral sac were not weighed because water was retained in the sac. Fish were classified as immature, gravid, running ripe, or spent by gross inspection of the gonads.

In a preliminary study, otoliths, cleithra, opercles, jaw bones, fin rays, and all the vertebrae were removed from a small number of fish. Afterwards only vertebrae No. 2-No. 7 were removed from the fish and were disarticulated and then stained in a solution of 4-8% KOH and Alizarin Red S. The stain reduced glare from the centrum surface and increased contrast

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between growth bands while KOH removed adherent flesh. Staining techniques of Hollister (1934), Galtsoff (1952), Daiber (1960), and La Marca (1966) were not effective in staining growth marks differentially. Puffer vertebrae have deeply concave centra and had to be sliced lengthwise in order to measure straight-line distances. Vertebrae No. 4 and No. 5 with the neural spines removed were placed dorsal surface up in a V-shaped slit in a wood block and were sliced with a hand-held razor blade. All vertebral measurements were made on vertebra No. 4 using an ocular micrometer in a dissecting microscope at 15× under reflected light. The marginal width or distance between the last annulus and the centrum edge was measured on the posterior segment of vertebra No. 4.

AGE DETERMINATION

Vertebrae and saccular otoliths exhibited growth marks, although only the growth marks on vertebral centra were both distinct and consistent. Growth marks on otoliths were ambiguous and could not be distinguished in larger fish. Cleithra, opercles, jaw bones, and fin rays exhibited no discernible growth marks.

Growth marks on northern puffer vertebrae formed distinct steps on the centrum surface which are best seen when a vertebra is rested on one end at a 45° angle from the vertical and is viewed looking down on the centrum face. The step is more opaque and its surface texture appears coarser under magnification in reflected light than the rest of the centrum. A narrow, dark, translucent ring appears along the inner edge of each step. The step and narrow dark band form a continuous ring on the centrum and constitute the annulus. Broad opaque bands with uniform surface texture lie between the narrower annuli. Together these features represent 1 yr's growth. Season marks on black bullhead, *Ictalurus melas*, vertebrae are narrow, translucent bands associated with a depression in the centrum surface and alternating with broad, opaque bands (Lewis, 1949). In contrast, narrow dark annual bands on channel catfish, *I. punctatus*, were usually associated with a ridge (Appelget and Smith, 1951).

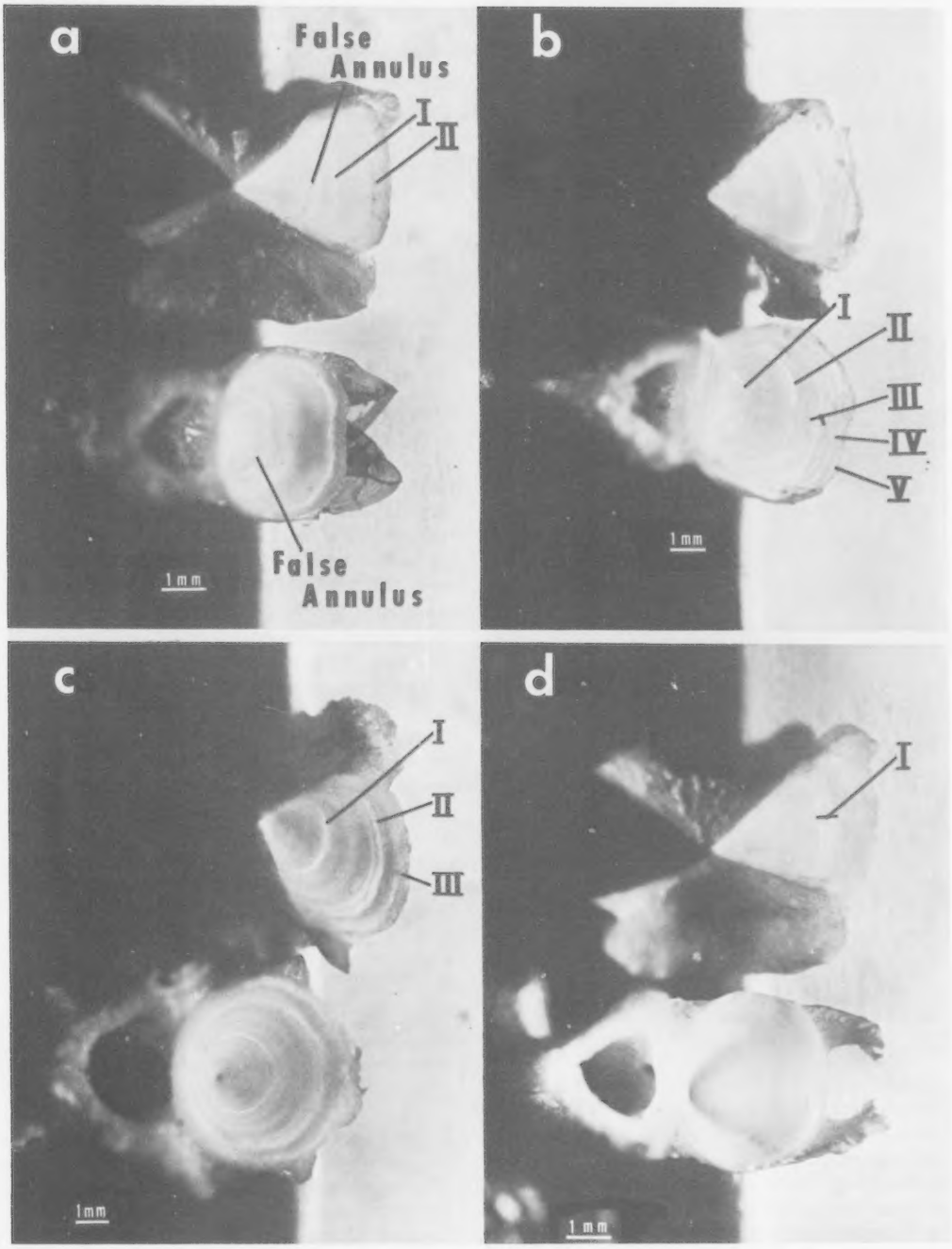
Five age groups of northern puffer were found by considering the marks on vertebrae to be annuli.

There was excellent agreement among vertebrae No. 3-No. 7 in the number and position of annuli. Age could not be assigned because of disagreement in less than 1% of the fish. However, age could not be determined in 7% of the fish because of false annuli, crowding of annuli at the centrum edge, and changes in the surface texture of centra in older fish. False annuli were faint dark bands which were not associated with a distinct step. Another extraneous mark was a shallow depression forming a continuous ring on the centrum which was not a definitive step. This feature was found on black bullhead vertebrae (Lewis, 1949). False annuli were most frequent in the first growth zone (Figure 1a). With increasing age, annuli became crowded at the centrum edge (Figure 1b), and the surface texture of centra became more coarse and irregular, especially near the edge (Figure 1c). However, there was no indication that annuli at the centrum edge were obscured by crowding in the 58 age III and 17 age IV fish examined.

VALIDATION OF THE ANNULUS

The annular step on vertebrae of the northern puffer met four of Hile's (1941) criteria for validating the annulus as a true year mark. First, a single annulus was formed each year. No annuli were present on vertebrae of yearlings in April and early May, but a distinct ring became visible at the outer edge of the centrum late in May when growth resumed (Figure 2). Annulus formation began in May, and by August most yearlings had formed an annulus (Figure 3). The fish taken in April with a single annulus and wide marginal width

FIGURE 1.—Vertebrae of the northern puffer: (a) vertebrae from a 2-yr-old northern puffer showing a false annulus adjacent to the first annulus, (b) vertebrae from a 5-yr-old northern puffer on which the third annulus appears double because of the expanded step, (c) vertebrae from a 3-yr-old northern puffer, (d) expanded annular step on the vertebrae from a 1-yr-old northern puffer.


a
False Annulus
I
II
1 mm
False Annulus
b
I
II
III
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V
1 mm
c
I
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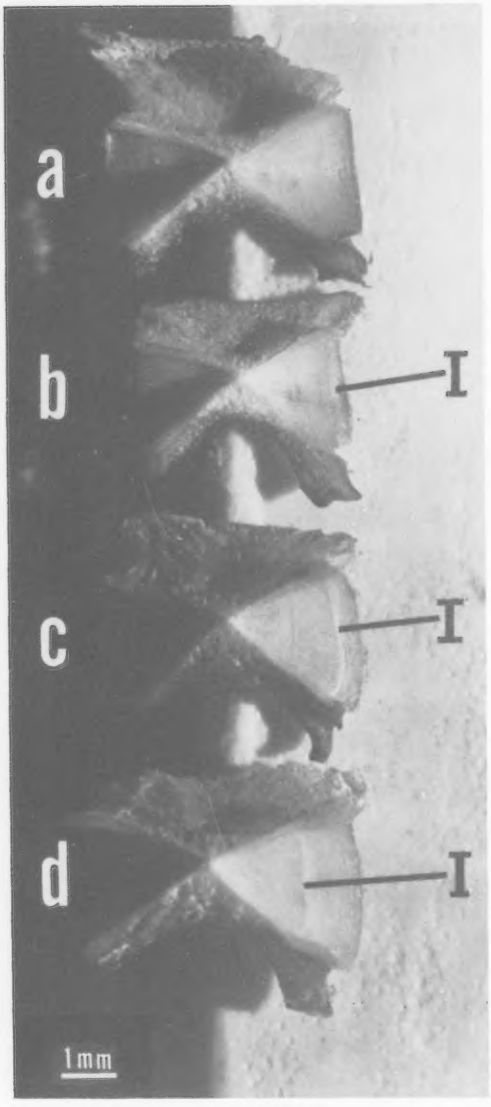

FIGURE 2. (left)—Vertebral sections of the northern puffer showing the increase in margin width after formation of the first annulus: (a) young-of-the-year female captured in November, (b) female captured in May with the first annulus just visible at the centrum edge, (c) age I male captured in September, (d) age I male captured in November.

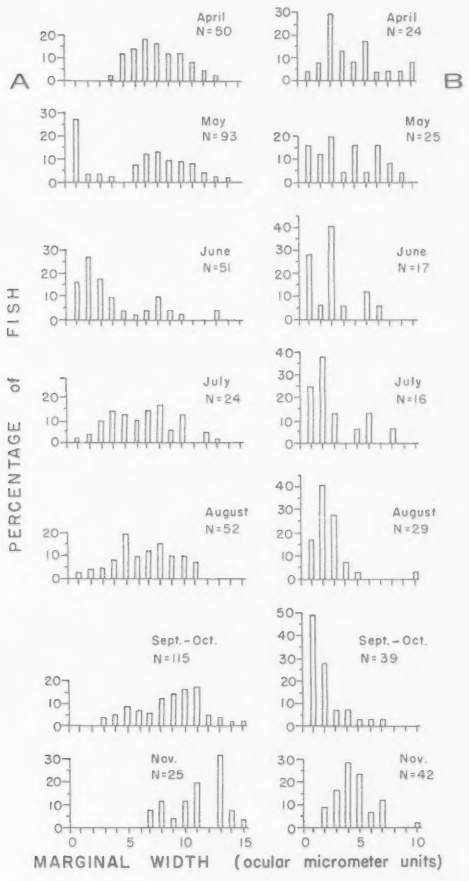

FIGURE 3.—Frequency distributions of margin widths (distance between the last annulus and the centrum edge) of vertebral centra from the northern puffer: (A) with a single annulus, (B) with two annuli.

(column A, Figure 3) were 2-yr-olds prior to formation of the second annulus. The greatest percentage of fish with the second annulus at the centrum edge occurred in September. Annulus formation on the centrum may take longer than on scales and otoliths because vertebrae are larger and structurally more complex. Yasuda (1940) showed that annuli on vertebrae of *Scombrops* sp. were formed 1.5 mo later than on otoliths. In older fish the length of time for annulus formation may be extended further because of the decreasing annual addition to

TABLE 1.—Calculated total length at end of each year of life of male and female northern puffer.

Age group	Number of fish		Mean length at capture (mm)		Mean calculated total length (mm) at end of year of life							
					1		2		3		4	
	M	F	M	F	M	F	M	F	M	F	M	F
I	190	315	181	200	133	151	—	—	—	—	—	—
II	88	99	204	235	125	141	183	208	—	—	—	—
III	22	32	224	256	125	128	178	194	208	237	—	—
IV	7	9	236	274	146	137	185	194	213	238	227	259
Weighted mean length					131	147	182	204	209	237	227	259
$S_{\bar{Y}}\, t_{.05}$					±2.5	±2.2	±3.5	±4.2	±6.8	±6.1	±18.4	±15.6
Length increment					131	147	52	58	27	33	19	22
Calculated length range					93-191	90-203	140-231	161-260	172-246	197-279	201-250	236-289
Measured length range					120-225	125-259	161-232	181-264	199-256	223-292	211-263	246-295

vertebral length as body length increments decrease.

The second criterion was met by the agreement of measured lengths with length at each age as calculated by the Lee method (Lagler, 1956) (Table 1). Mean weighted lengths at each age coincided closely with the measured length for fish 1 yr younger because most fish were taken in the fall after the growing season and in late spring before the growing season. Total vertebral length and distance between annuli across the center of the vertebra were used to calculate lengths. Measurements were made along the shortest straight line connecting the approximate midpoints of annuli and the centrum edge (Figure 4). The distance between annuli could not be measured with certainty in 5% of the fish because the annular step was expanded into a broad, opaque shelf without a distinct end point (Figure 1d). The plot of body length on vertebral length was approximately linear, and the regression equation was $L = 27.52 + 3.28V$ with a significant correlation coefficient of 0.9827 where L is total length in millimeters and V is vertebral length in ocular micrometer units.

The third and fourth criteria were met by the correspondence of peaks in the length-frequency plots for each age group with peaks in the plot of the entire sample and by the regular increase in number of annuli with increasing body length (Figure 5). Overlap in mean body length among age groups was caused by early summer annulus formation in yearlings coupled with an extended period of annulus formation in older age groups. The wide range of lengths attained in the first growing season also contributes to the observed overlap of body lengths. The biomodal distribution of females in age group I was caused by the great number of fish larger than 210 mm taken in April and May from culled and sorted commercial pound net catches. Throughout the rest of the sampling period, the majority of fish came from unculled pound net and haul seine catches.

Therefore, the annulus on northern puffer vertebrae has been validated based on agreement with these criteria.

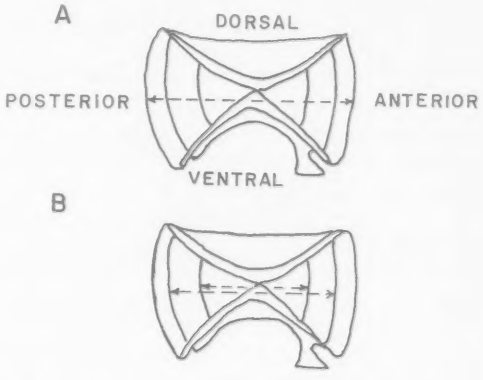

FIGURE 4.—Measurements taken on vertebral sections which were used in calculating length at age: (A) vertebral length, (B) distance between annuli across center of vertebra.

GROWTH

Young-of-the-year which were first collected in June from shallow eelgrass (*Zostera marina*) beds in the York River averaged 28 mm in length. Young-of-the-year in the fall of 1970 ranged from 88 to 184 mm (Table 2). The November sample came from a culled pound net catch; therefore, 160 to 184 mm is not a true indication of the length range after the first growing season. A better estimate is 83 to 195 mm based on lengths of yearlings without an annulus taken in April and May with a trawl and from unculled pound net catches. This corresponds closely to the calculated range of lengths at age I for all fish, 90-203 mm (Table 1). In December a live 37-mm juvenile was found floating at the surface near the mouth of the York River. Several fish of this size were collected in October on the east side of Chesapeake Bay during 1968 and 1969 by personnel of Virginia Institute of Marine Science. It is not known whether these small fish were hatched late in the season in Chesapeake Bay or were southern migrants from more northern spawning stocks.

The von Bertalanffy mathematical expression of growth as outlined by Ricker (1958) closely fits the weighted mean length at each age for age groups I to IV (Figure 6). The weighted mean length for age group I was calculated from age groups II, III, and IV because commercial gear is selective for the larger fish of age group I. Females were larger than males at all ages. Covariance tests (Ricker, 1958; Mottley, 1941; Snedecor, 1956) on the Ford-Walford lines for males and females indicated a significant difference in the lengths attained by males and females in the first growing season, but the difference in growth after the first season was not significant at the 5% level. The decrease in yearly increment of length was similar for both sexes (Figure 6).

REPRODUCTION

Differences between testes and ovaries in vascularization and size became apparent in

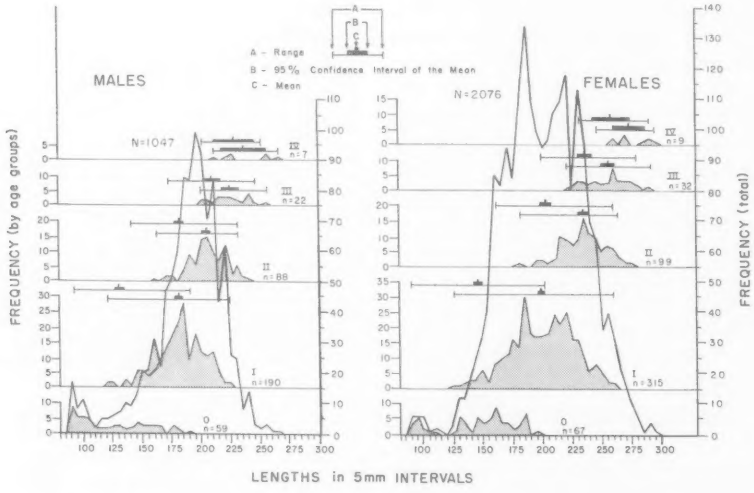

FIGURE 5.—Length-frequency distributions of the northern puffer (shaded polygons for each age group; unshaded polygon represents fish from the entire 1970 collection; distribution characteristics for each age group are shown above polygons with calculated lengths above measured lengths).

TABLE 2.—Length-frequency of young-of-the-year northern puffer.

Total length (mm)	June	July	Aug.		Sept.		Oct.		Nov.		Dec.
	sex unknown	sex unknown	M	F	M	F	M	F	M	F	sex unknown
18- 22	1										
23- 27	6										
28- 32	3										
33- 37	1										
38- 42											1
43- 47											
48- 52											
53- 57											
58- 62		1									
63- 67		1									
68- 72		2									
73- 77											
78- 82											
83- 87											
88- 92		2			5	4					
93- 97					2	6					
98-102		3	1		4	2					
103-107					1	1					
108-112			1			1					
113-117					1	1					
118-122					1						
123-127					1						
128-132					1	3					
133-137					2	3					
138-142					2	3					
143-147					1	4	1	1			
148-152						1					
153-157											
158-162									1	1	
163-167						1		1		1	
168-172										2	
173-177										1	
178-182										1	
183-187										2	
N	11	9	2		21	30	1	2	1	8	1

young-of-the-year by early September. Both sexes reached sexual maturity by the second growing season. In the spring the gonads of fish as small as 88 mm contained either milt or ova. Running ripe males were first obtained during the last week of May. Females were gravid during May but from June through the first week of July they were found in all three conditions, gravid, ripe, and spent. Few running ripe females were taken. Males were running ripe longer than females and may spawn a greater number of times.

By late July gonads of most fish taken from the mouth of the York River, Mobjack Bay, and lower Chesapeake Bay were spent and in recovery stages. However, males taken from the mouth of the Rappahannock River in mid-August were still running ripe, and many females were gravid. Welsh and Breder (1922) took ripe females along the New Jersey coast from July 30th to August 27th. Wheatland (1956:296-297) reported northern puffer spawning from late May until August in Long Island Sound. Time and duration of northern puffer spawning appears variable within Chesapeake Bay and along the middle Atlantic coast. By September gonads of puffers from lower Chesapeake Bay were in various stages of recovery. Neither milt nor developing ova were visible during October and November.

The ratio of males to females in May and November was approximately 1:1. However, females were consistently more abundant throughout the summer and early fall. During this period the ratio of males to females was 1:3. Males were least abundant during the peak of spawning in June and July. This change in the sex ratio may be related to reproductive behavior.

WEIGHT-LENGTH RELATIONSHIP

Logarithmic functions describing the exponential increase in weight with increasing length according to sex and gonadal condition were calculated (Figure 7). These plots indicate that logarithmic transformation of weight and length give a linear relation. About 89 to 99% of the variation in weight is associated with variation in length of pre- and post-spawning puffers of each sex. Puffers of both sexes were heavier after recovery from spawning (late July to November) than fish of comparable length before spawning (April to early July). Covariance tests (Mottley, 1941) indicated that this difference in weight was not significant in females but was in males at the 5% level. A large increase in muscle and liver tissue occurred during the growing season but was not quantified. By November fish appeared more robust and had larger livers than in April.

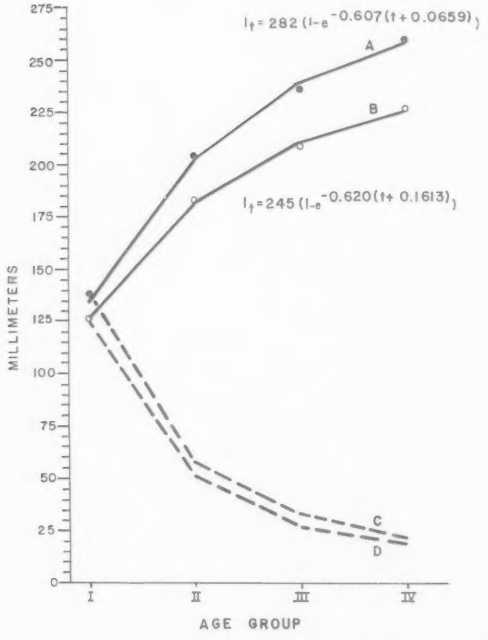

FIGURE 6.—Growth curves of female (A) and male (B) northern puffer fitted by the von Bertalanffly growth equation and plots of increments in length of females (C) and males (D) (circles represent calculated lengths).

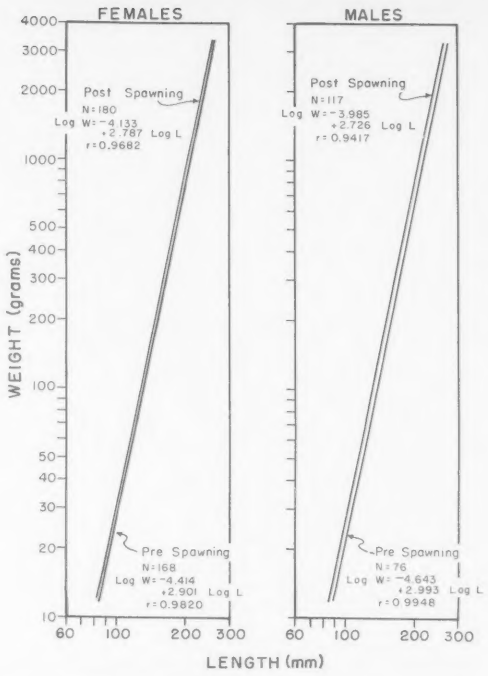

FIGURE 7.—Weight-length relationships for northern puffers in postspawning condition (late July to November) and in prespawning condition (April to early July).

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PATTERN, NUMBER, VARIABILITY, AND TAXONOMIC SIGNIFICANCE OF INTEGUMENTAL ORGANS (SENSILLA AND GLANDULAR PORES) IN THE GENUS *EUCALANUS* (COPEPODA, CALANOIDA)

ABRAHAM FLEMINGER[1]

ABSTRACT

Methods for study of bilaterally symmetrical, serially homologous sets of integumental organs comprising hair, peg, and pit sensilla and the pores of integumental glands as well as their number and distribution in the genus *Eucalanus* are described.

A survey of these organs was carried out on geographically representative samples of the 17 discrete populations I recognize as valid species in the genus. The survey concentrated on adult females, but smaller numbers of adult males and some younger copepodid stages were also examined. Numbers and arrangement of these organs, estimates of variability, and their relationship to total length were established for each species. Phenetic similarity in integumental organ arrangement is shown to concur with other morphological features within the genus. Comparison is also made between number and arrangement of integumental organs and the geographical relationships among the members in each species group. Several new species in the attenuatus group are described on the basis of integumental organs and geographical distribution. A preliminary study of geographical variation in the circumglobal, broadly tropical species *E. subtenuis* is used to estimate the general complexity of genetic control and the use of these organs to study gene flow and population variability in planktonic species.

The integument of arthropods bears numerous organs that fall into two general classes: sensory receptors or sensilla, and glands. Sensilla are composed of one to several sensory neurons and generally two accessory cells, the latter forming the external features which may be in the form of an outgrowth, i.e., a hair, a cone, or a peg, or an ingrowth such as a pit or plate organ with sensory cell bodies located underneath (Laverack, 1969; Schneider, 1969; Stürckow, 1970). The regular presence of sensilla containing nerve fibers has been demonstrated histologically in a variety of different copepods (e.g., Fahrenbach, 1962; Elofsson, 1971).

In terrestrial arthropods integumental glands are highly variable in number, in distribution, and in morphological detail (Eisner and Meinwald, 1966). Integumental glands described from copepods tend to be rather simple sacs underlying the integument and communicate with the environment via a simple pore penetrating the integument (e.g., Clarke et al., 1962; Fahrenbach, 1962; Park, 1966).

On the body of copepods as in mystacocarids and other arthropods, sensilla and glands are in general distributed in bilaterally symmetrical patterns that are somewhat redundant on successive body segments, i.e., they appear to be serially homologous (Sewell, 1929, 1932, 1947; Fahrenbach, 1962; Hessler, 1969). It is highly probable that chemical communication via integumental organs, a widespread means for exchanging information among arthropods and vertebrates (e.g., cf. Johnston, Moulton, and Turk, 1970) is essential to copepods. Dioecious and nonparthenogenetic copepods must locate and correctly identify a potential mate without visual aids. This search and contact procedure is mediated by pheromones in *Eurytemora* and called "mate-seeking behavior" (Katona, 1973). Moreover successful culmination of the mating act requires attachment of the spermatophore

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that permits passage of the sperm into the female's seminal receptacles (Wolf, 1905; Neubaur, 1913; Heberer, 1932; Fahrenbach, 1962).

Integumental organ systems are used widely in arthropod systematics. Indeed, in some groups, as for example, mosquitoes, dependence upon chaetotaxy is essential. A unique and particularly interesting application devised to permit identification of the fossilized remains of chydorid cladocerans in extinct lake sediments utilizes the number, size, and arrangement of integumental pores (Frey, 1959, 1962).

Despite repeated mention of integumental organs in the early copepod literature, attempts to apply them to study of marine species are rare. Notable exceptions must include With's (1915) detailed accounts of the sensilla surrounding the oral region for a number of species collected in North Atlantic samples. Sewell showed considerable interest in the general distribution of body integumental organs in planktonic copepods. His observations made on a broad variety of species are presented in scattered notes, remarks, and illustrations within the context of his faunal studies on Indian Ocean calanoids (1929, 1932, 1947). Unfortunately, the diminutiveness of these organs, Sewell's omission of methods for study, and a critical estimate of their reliability contributed to their neglect by subsequent workers. Two studies on bioluminescence in planktonic copepods (David and Conover, 1961; Clarke et al., 1962) call attention to the potential value of luminescing integumental glands for identifying the species of living specimens.

Conventional taxonomic systems organizing diversity among calanoid copepods are strongly dependent upon sexually modified structures of the adult (copepodid stage VI) sometimes assisted by nonsexual morphological or meristic features in the adult condition, as for example, spination and setation of appendages, segmentation of appendages, and segmentation of body tagmata. These sources of diagnostic information serve all hierarchial levels, species to family. Due to the nature of calanoid ontogeny, all of these structures assume their definitive state only in sexually mature adults. Thus, juveniles lie outside of existing systems, males and females are only rarely served by the same system, and genera that are relatively undistinguished in sexually modified structures tend to be "taxonomically difficult."

The primary purpose of this paper is to demonstrate the potential significance of sensilla and the pores of integumental glands on the body tagmata to the systematics and phylogeny of calanoid copepods. From a survey of these organs in the genus *Eucalanus*, their numbers and arrangements provide an objective basis for grouping related species, for distinguishing between sibling species, for relating adults of either sex to their respective species despite the elimination of other common characters by sexual dimorphism, for aiding in the specific identification of late immature copepods, and for the determination of regionalized cohorts that apparently lack unrestricted gene flow with morphologically similar cohorts in other regions.

REMARKS ON THE GENUS *EUCALANUS* DANA, 1853

Eucalanus is a universally familiar marine genus of eucalanid copepods. It contains primary consumers that form a conspicuous part of the epiplanktonic and uper mesoplankton in low to middle latitudes; some of the species are primarily oceanic, others are neritic. Within its habitat many of the species tend to be among the most abundant and largest (adult total length ranges from about 3 to 7 mm) of the regional copepod fauna. Since the inception of the genus for *E. attenuatus* (Dana, 1853), about 25 nominal species have been proposed. Contributions by Giesbrecht (1892), Johnson (1938), and Vervoort (1946, 1963) provide the framework for the genus and its taxa. The current world literature indicates 12 nominal species in active use. Two are represented by two subspecies each, yielding a total of 14 widely accepted taxa.

Though *Eucalanus* is a morphologically distinctive genus and its species are widespread and relatively abundant, frequent questions and confusion about the validity and rank of its nominal species and subspecies tarnish its literature. Difficulties with the identification

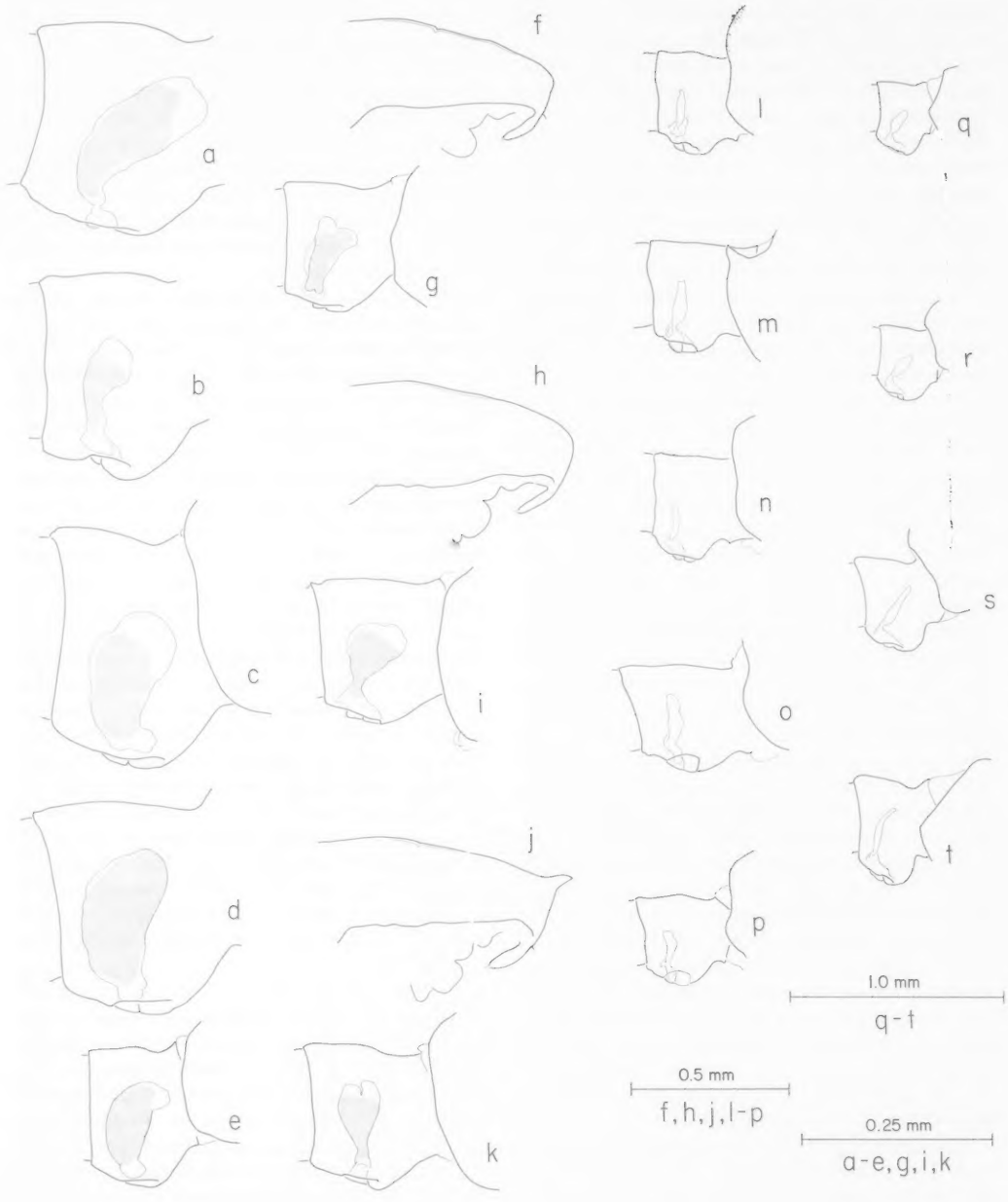
of the species emanate largely from the absence of distinctive sexually modified appendages, the few available meristic characters in setation and the widespread dependence of the existing taxonomic system upon relatively subtle shapes and proportions of segments and tagmata unsupported by rigorous estimates of variability. Difficulties and inconsistencies associated with the rank of the taxa in the genus *Eucalanus*, notably in the elongatus group, might be the product of several factors: e.g., the lack of accurate data on geographical distribution, uncertainties about the significance of morphological differences among the subspecies, the widespread lack of an adequate basis for viewing the planktonic taxon in the perspective of a biological population.

For example, questions or expressed doubts challenge the validity of separating *E. pileatus* from *subcrassus*, and the two have often been confused with *monachus* (Deevey, 1960; Grice, 1962; Vervoort, 1963; Lang, 1965). Confusion about *subtenuis* appears to trouble some (Fukase, 1957). Awareness of variation and taxonomic complexity within the nominal species *attenuatus* has been noted frequently (Sewell, 1947; Tanaka, 1956; Brodsky, 1962; Lang, 1965; Park, 1968), and similar questions must be raised regarding *dentatus* (Fleminger, unpublished data). Finally, a point must be made with regard to the elongatus complex. Three decades have passed since Johnson's (1938) perspicacious revision based on so few data, decades of increasing oceanographic activity and the accumulation of geographical and morphological observation on these common forms. Considering our increased experiences and understanding the logic of justification for the general practice of regarding *inermis* as a full species but continuing the two subspecies of *elongatus* and the two subspecies of *bungii* escapes me. On the basis of both morphology and geography the known similarities and differences between *inermis* and its two cognates and those between the subspecies of each of these cognates are about equal.

As part of an unpublished doctoral dissertation, Lang (1965) presented a taxonomic review and study of the distribution of *Eucalanus* in the Pacific Ocean based on plankton samples from the Scripps Institution of Oceanography Zooplankton Collections. Lang's data on the elongatus complex, published in 1967, contributed appreciably to our knowledge of geographical relationships among its populations. Though providing considerable evidence favoring extension of the revision initiated by Johnson (1938), his use of subspecies was retained. Expressed dissatisfaction with separation of *pileatus* and *subcrassus* and the considerable variation encountered in *attenuatus* s.l. were noted in the unpublished portion of Lang's dissertation.

My attempts to strengthen the *Eucalanus* section of Lang's manuscript for publication using the material on hand to clarify unresolved issues were unsuccessful. Two issues emerged: Resolution of the difficulties depended on 1) expanding geographical representation to encompass the world ocean and 2) the need to develop more reliable morphological characters for distinguishing the reproductively isolated populations within the genus. As conditions permitted, I gathered geographic records and specimens of *Eucalanus* in conjunction with global studies on other calanoid genera including *Clausocalanus* and *Pontellina* (Frost and Fleminger, 1968; Fleminger and Hulsemann, in press). In addition, I began to examine various structures of *Eucalanus* at relatively high magnifications (200× to 600×). Useful characters were found in the female genital segment, especially in the shape and arrangement of the seminal receptacles, and in the male fifth legs. For example, general similarities in the seminal receptacles provided a promising basis for phylogenetic groupings within the genus and a dependable means for separating at least some of the species of the pileatus group (Figure 1).

In the course of my survey, distinctive patterns in the distribution of integumental organs on the urosome became apparent. Recall of Sewell's (1947) use of these features to support his separation of *attenuatus* and *pseudattenuatus* prompted development of procedures described below to map integumental organs on dorsal and lateral surfaces of all body segments. The results provided the means for separating regional populations, species, and species


a
b
c
d
e
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g
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j
k
l
m
n
o
p
q
r
s
t
1.0 mm
q-t
0.5 mm
f, h, j, l-p
0.25 mm
a-e, g, i, k

FIGURE 1.—Genus *Eucalanus*. Genital segment, lateral view, female—**a.** *subtenuis* (Downwind 28); **b.** *mucronatus* (Monsoon 11); **c.** *crassus* (*Alaska* 4-36); **d.** *longiceps* (Monsoon 24); **e.** *monachus* (*Alaska* 5-7); **g.** *pileatus* (Lusiad VII Freetown); **i.** *subcrassus* (Lusiad II H-1); **k.** *dentatus* (Naga S11A 61-198); **l.** *elongatus* (Naga S11A 61-127); **m.** *hyalinus* (TRANSPAC 10 B); **n.** *inermis* (Muddauber 137-1); **o.** *bungii* (TRANSPAC 65 B); **p.** *californicus* (5606 50.80); **q.** *attenuatus* (EASTROPAC A 207); **r.** *sewelli* (*Atlantis* II-31-119); **s.** *parki* (Boreas 19); **t.** *langae* (Monsson 24). Anterior portion of head, lateral view, female—**f.** *pileatus* (Lusiad VII Freetown); **h.** *subcrassus* (Lusiad II H-1); **j.** *dentatus* (Naga 61-198). The shaded areas indicate the extent of sperm in the seminal receptacle. Positions for stations mentioned are listed in Snyder and Fleminger (1965, 1972).

groups within the genus and concurred with the evidence derived from study of the seminal receptacles. Greater appreciation of the reproductively isolated populations within *Eucalanus* (Table 1) also revealed the compelling need for much additional work on finer details to complete a satisfactory account of each species. The four geographical forms of *attenuatus* s.l. require comparative study of conventional morphological features in both sexes. Their geographical distributions should be amplified by reexamination of the great number of records and sorted specimens now in hand recorded collectively under *attenuatus* s.l.

Evidence of geographical variation in *subtenuis*, described below, requires additional study and should be examined in the context of co-occurrence with its sibling congener, *mucronatus*. Also, closer geographical scrutiny should be made of other widely ranging species showing broadly neritic habitat preferences such as *crassus* and *pileatus*.

Realization that the significance of integumental organs in copepods overshadows and holds more widespread interest than the genus *Eucalanus* is the basis for presenting the survey of sensilla and pores within the framework of an incomplete taxonomic review. Completing the global account of *Eucalanus* first would impose a long and unnecessary delay. Based on seminal receptacles, geography, and integumental organs, the essential diversity within the genus is now unmistakably clear. Details still

TABLE 1.—Author's provisional list of valid species and phylogenetic groupings comprising the genus *Eucalanus*. Summarized distribution and biogeographic assignment based on records confirmed by author.

subtenuis group:
1. *E. subtenuis* Giesbrecht, 1888. Broadly Tropical, circumglobal[1] in eutrophic oceanic waters; epiplanktonic. Figure 9e.
2. *E. mucronatus* Giesbrecht, 1888. Tropical, Indian Ocean to western Pacific in equatorial circulation systems[2]; epiplanktonic. Figure 9d.
3. *E. crassus* Giesbrecht, 1888. Tropical-subtropical, circumglobal in eutrophic broadly neritic waters; epiplanktonic. Figure 9a.
4. *E. longiceps* Matthews, 1925. Boreal-temperate, circumglobal, Southern Hemisphere West Wind Drift system (= Southern Ocean Transition zone); epiplanktonic? Figure 9b.
5. *E. monachus* Giesbrecht, 1888. Tropical-subtropical, Atlantic, broadly neritic; subsurface epiplanktonic. Figure 9c.

pileatus group:
6. *E. pileatus* Giesbrecht, 1888. Tropical-subtropical, circumglobal, coastal- neritic; epiplanktonic. Figure 11a.
7. *E. subcrassus* Giesbrecht, 1888. Tropical, Indo-Pacific, broadly neritic; epiplanktonic. Figure 11c.
8. *E. dentatus* Scott, 1909. Tropical, Austral-Asian seas; coastal epiplanktonic. Figure 11b.

elongatus group:
9. *E. elongatus* (Dana, 1849). Tropical, Indian Ocean to western Pacific in equatorial circulations; epiplanktonic? Figure 13b.
10. *E. hyalinus* (Claus, 1866). Tropical-subtropical, circumglobal especially in eutrophic, oxygenated waters adjacent to boundary currents; deep epiplankton to upper mesoplankton. Figure 13c.
11. *E. inermis* Giesbrecht, 1892. Eastern Tropical Pacific in eutrophic, low oxygen water; deep epiplankton to upper mesoplankton. Figure 13a.
12. *E. bungii* Giesbrecht, 1892. Boreal-subpolar, North Pacific, and Bering Sea; epiplanktonic to upper mesoplanktonic.
13. *E. californicus* Johnson, 1938. Temperate, North Pacific, West Wind Drift system (= North Pacific Transition zone); deep epiplanktonic to upper mesoplanktonic. Figure 13d.

attenuatus group:
14. *attenuatus* (Dana, 1849). Tropical, Indo-Pacific equatorial circulation systems; epiplanktonic. Figure 15d.
15. *sewelli* sp.n. Tropical-subtropical, circumglobal; epiplanktonic. Figure 15c.
16. *parki* sp.n. Temperate, North Pacific, West Wind Drift system (= North Pacific Transition zone); deep epiplanktonic to upper mesoplanktonic. Figure 15a.
17. *langae* sp.n. Temperate, circumglobal, Southern Ocean West Wind Drift system (= Southern Ocean Transition zone); deep epiplanktonic and upper mesoplanktonic. Figure 15b.

[1] Evidence of three regionalized populations: Eastern Tropical Pacific; Tropical Indian Ocean to western Tropical Pacific; Tropical Atlantic.
[2] Two questionable records from Tropical Atlantic: Florida Current (Owre and Foyo, 1967) and Gulf of Mexico (Fleminger, unpublished data). Forehead pointed but basal segment of mandible with two setae.

TABLE 2.—Adult female *Eucalanus*: collecting localities and numbers of specimens surveyed for sensilla and pores. All samples taken with open nets ½ m or larger in diameter at the mouth and towed horizontally or obliquely at epiplanktonic depths.

Cruise or ship	Station	Latitude	Longitude	Date	Species*															
					A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
Afram[1]	F-1	14°00'N	17°30'W	?			5		2												
Alaska[2]	4-36	23°31'N	86°44'W	24 Jan 52	2																
	5-9	26°00'N	87°32'W	26 May 52																2	
	11-5	29°07'N	88°47'W	30 May 53					3	2											
Arctic Exped.	1310(4)	38°49'N	168°03'W	19 Jul 47													5				
Atlantis 11-31[3]	15	24°42'N	49°42'W	19 Jan 67																1	
	31	20°07'N	20°36'W	27 Jan 67			3														
	33	19°21'N	16°52'W	28 Jan 67					3												
	34	18°35'N	16°59'W	28 Jan 67	4		2			2											
	35	17°54'N	17°20'W	28 Jan 67			5														
	36	15°45'N	17°45'W	29 Jan 67					7												
	43	08°08'N	19°48'W	9 Feb 67					5											7	
	45	05°41'N	21°29'W	11 Feb 67																1	
	46	04°09'N	22°45'W	11 Feb 67											1					1	
	48	00°56'N	25°20'W	12 Feb 67					2												
	51	00°07'N	28°43'W	14 Feb 67					2												
	74	29°11'S	40°06'W	12 Mar 67																3	
	80	26°20'S	46°05'W	28 Mar 67																2	
	119	30°23'N	64°17'W	30 Apr 67																1	
	122	35°12'N	67°15'W	2 May 67																2	
	123	36°59'N	68°50'W	2 May 67											3						
Azul I	F-1	23°38'N	109°36'W	5 Sep 62					4												
Boreas	19	41°57'N	165°06'W	2 Feb 66													1	2			
	64	58°21'N	168°57'E	15 Feb 66												5					
	148	48°55'N	157°55'E	12 Mar 66												4					
Bureau of	F1832	34°02'S	17°44'E	8 May 62					1										1		
Sea Fisheries[4]	A2000	33°04'S	17°16'E	8 Sep 62											3						
	A2003	33°05'S	17°47'E	8 Sep 62					1												
	90.28D	33°28'N	117°47'W	13 Jun 52													3				
CalCOFI 5206	120.50	27°33'N	115°52'W	18 Apr 55													5				
5504	144G.15	24°28'N	110°28'W	24 Aug 57																2	
5708	137.30	25°20'N	112°45'W	10 Jul 58									2								
5807	PT 18	22°31'N	105°53'W	26 Aug 61						5		5									
6108	27	03°30'S	121°54'W	9 Feb 53					2												
Capricorn	31	06°31'S	124°41'W	13 Feb 53																	3
	32	07°58'S	124°11'W	14 Feb 53									1								
	5	15°41'N	64°12'W	14 Jun 65					2												
Chain 49[3]	9	19°52'N	69°57'W	16 Jun 65					7												
	13	14°48'N	68°09'W	26 May 66																1	
Chain 60[3]	15	12°58'N	73°34'W	28 May 66			5														
	4	42°33'N	162°09'W	17 Jul 56											1			4			
Chinook	8	40°28'N	173°04'W	3 Aug 56											2			4			
	NT 3	22°28'N	177°21'E	5 Apr 68					1												
Circe	NT 8	17°29'N	141°38'E	16 Apr 68					1												
	NT 11	05°11'N	123°58'E	20 Apr 68																1	1
	NT 14	08°28'N	118°24'E	23 Apr 68				5						2							
	NT 15	07°16'N	115°20'E	24 Apr 68					4												
	NT 16	05°39'N	112°39'E	25 Apr 68											2						
	NT 25	19°04'N	87°47'E	17 May 68																	1
	NT 27	09°46'N	83°31'E	23 May 68																	2
	NT 30	07°27'N	77°42'E	27 May 68																4	
	NT 33	19°42'S	63°12'E	28 Aug 68					2												
	Camera 3	26°28'S	46°04'E	29 Sep 68					1												
	Dm 2.75.63	11°00'S	110°00'E	26 May 63							2										
Diamantina[5]	36	06°05'N	49°53'E	16 Aug 64																	3
Dodo VI	49	10°19'N	53°11'E	20 Aug 64								2									
	54	10°23'N	51°43'E	22 Aug 64	2																
	55	10°14'N	51°19'E	22 Aug 64				4						5							
	55-15	09°45'N	51°31'E	23 Aug 64					1											1	
	60	11°58'N	55°11'E	26 Aug 64					2	1		7		1						2	
	86	12°00'S	55°55'E	5 Sep 64								5									
Downwind	19B	46°25'S	123°38'W	4 Dec 57		7															
	20C	44°36'S	112°08'W	10 Dec 57															1		
	22A	40°39'S	92°02'W	17 Dec 57															1		
	24	34°30'S	79°30'W	20 Dec 57																2	
	28	27°08'S	72°02'W	31 Dec 57					3				3							3	
EASTROPAC	J 087	01°34'N	105°00'W	26 Feb 67					3												
	A 207	13°23'S	126°00'W	19 Feb 67																	3
Eastropic	82	08°00'N	104°00'W	9 Dec 55									6								

TABLE 2.—*Continued*

Cruise or ship	Station	Latitude	Longitude	Date	Species*														
					A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
El Golfo I	I CN2	24°38′N	109°22′W	14 Nov 63									2								
	II CD1	25°35′N	110°14′W	17 Nov 63									1								
	VI AN2	28°37′N	112°56′W	25 Nov 63																1	
El Golfo II	XIV B2D1	26°31′N	111°03′W	22 May 65																1	
EQUAPAC	H 20	10°00′S	163°00′E	17 Aug 56																	3
	S 1	20°43′N	158°27′W	21 Aug 56				5													
	S 20	00°51′N	167°14′W	29 Aug 56					10												
	S 21	00°02′N	166°59′W	29 Aug 56																	1
	S 23	01°55′S	166°52′W	30 Aug 56																	2
Gascoyne[3]	G1.24.63	15°31′S	110°00′E	10 Feb 63																	2
	G1.28.63	21°26′S	110°01′E	12 Feb 63					3											2	
	G1.29.63	23°10′S	110°00′E	12 Feb 63					2												
Gilf[6]	2-74	34°24′N	75°36′W	10 May 53					2												
	8-9	28°20′N	79°48′W	12 Sep 54					3												
Lusiad II	H 1	01°16′N	103°52′E	28 Jun 62							6										
	H 7	06°58′N	79°50′E	28 Aug 62						3											
	29	05°02′N	53°01′E	31 Jul 62										1							
	45	05°00′S	62°00′E	14 Aug 62						1		4									
	51	00°57′S	62°19′E	17 Aug 62										1							
Lusiad V	46	00°02′N	58°52′E	30 Mar 63					4												
	48	00°01′S	63°00′E	1 Apr 63																	2
	50	00°00′	67°02′E	2 Apr 63					4												
	54	00°08′N	74°59′E	4 Apr 63				2	2					1							
	64	04°54′N	92°02′E	19 Apr 63										1							
	94	02°01′N	53°02′E	5 May 63										1							
Lusiad VII	75 H 7	00°28′S	10°51′W	4 Jul 63					6												
	MWT 14	32°29′S	09°04′E	6 Jun 63		1													4		
	MWT 19	31°11′S	00°56′E	9 Jun 63											2				5		
	MWT 79	00°55′N	11°29′W	6 Jul 63																1	
	Freetown	08°30′N	13°17′W	11 Jul 63						3											
Monsoon	7	09°11′S	127°33′E	22 Oct 60				2			2			2							
	9	13°19′S	109°35′E	7 Nov 60										2							
	11	11°15′S	103°32′E	20 Nov 60										2	1						
	13	17°01′S	93°29′E	25 Nov 60					1												
	22	37°50′S	85°22′E	26 Dec 60		2									2				1		
	24	39°18′S	119°51′E	9 Jan 61		2									2				1		
	26	64°11′S	165°56′W	13 Feb 61																	1
	31	32°35′S	160°56′W	8 Mar 61											2						
Naga	61-13	08°18′N	104°42′E	13 Jan 61								4									
	61-124	10°12′N	103°50′E	10 Feb 61								2									
	S10 61-107	09°19′N	103°58′E	10 Feb 61						4		4									
	S11A 61-198	09°11′S	115°33′E	27 Mar 61				2			11									2	2
	S11B 61-268	03°20′S	127°21′E	26 Apr 61																2	1
NORPAC	1 H	45°58′N	134°22′W	30 Aug 55												2	2				
	24-42H	40°26′N	146°37′W	21 Aug 55											1			6			
Scan	IV-1	33°49′N	139°10′E	15 Jun 69					5												
Shellback	90	06°01′S	95°46′W	26 Jun 52											2						
	109	03°41′S	81°30′W	4 Jul 52									1								
T. Washington	13	11°16′N	64°10′W	2 Jan 66					6												
TO-58-1 (Scot)	35	09°45′N	96°04′W	7 May 58																	4
Transpac	10 B	38°22′N	141°23′W	31 Jul 53											3						
	32 B	52°29′N	176°09′W	15 Aug 53												3					
	64 B	46°54′N	153°55′E	15 Sep 53												1					
Troll	40	31°10′N	128°48′E	10 Apr 55	3							2									
	45 A	31°17′N	137°29′E	12 Apr 55													7			1	1
	56	34°21′N	138°29′E	13 Apr 55					3												
Zetes	14	39°00′N	154°58′W	17 Jan 66														2			

* Species code:

A	*crassus*	G	*dentatus*	M	*californicus*
B	*longipceps*	H	*subcrassus*	N	*parki*
C	*monachus*	I	*inermis*	O	*langae*
D	*mucronatus*	J	*elongatus*	P	*sewelli*
E	*subtenuis*	K	*hyalinus*	Q	*attenuatus*
F	*pileatus*	L	*bungii*		

Unless identified by footnotes the samples are from the Marine Invertebrate Collections of Scripps Institution of Oceanography.

[1] University of Rhode Island.
[2] National Marine Fisheries Service, Galveston Laboratory.
[3] Woods Hole Oceanographic Institution.
[4] Bureau of Sea Fisheries, Cape Town, Republic of South Africa.
[5] Commonwealth Scientific and Industrial Research Organisation, Cronulla, Australia.
[6] National Marine Fisheries Service, Beaufort Laboratory.

remaining to be analyzed will not affect basic conclusions to be drawn about the sensilla and pores in *Eucalanus*. For purposes of this paper nomenclatural recommendations have been limited to an essential minimum. The species I recognize are summarized in Table 1. Aside from the integumental organs and dorsal and lateral views of the body, description of other characters is restricted to a few basic features (Figure 1).

Functional significance aside, the diagnostic qualities of body patterns of pores and sensilla should be examined in the Copepoda on a broad front.

MATERIALS AND METHODS

Systematic analysis of sensilla and pores was carried out routinely on adult females of all *Eucalanus* populations known to me (Table 1). Numbers of specimens and collecting localities are shown in Table 2. Sample size varied for each species according to its geographical distribution, the overall frequency of variation, number and arrangement of sensilla and pores, and the availability of specimens. The number of regularly occurring pores and sensilla on the body of a specimen is large, ranging from 80 to 140 depending on the species, and their unvarying arrangement in strongly patterned, bilaterally symmetrical arrays eliminated the need for examining large numbers of specimens in all but one case. Specimens were selected at random from within each zooplankton sample, but collecting localities were deliberately chosen to represent the known distribution of the species; i.e., as material on hand permitted representative specimens of each species were selected for examination from peripheral, intermediate, and central localities. Observations on adult males and on copepodite stages IV and V were also made on all species but were ordinarily limited to only two to four specimens each.

Sensilla and pores are exceedingly difficult to observe in *Eucalanus* using conventional light microscopy without staining and clearing specimens. Two simple methods were employed in this study. One served in examining general external features of the various types of sensilla and their proximity to glandular pores. Specimens were immersed for about 24 h in a combined clearing agent and stain, consisting of 9 parts lactic acid and 1 part of a 1% solution of chlorazol black E (CBE) in 70% ethanol. Specimens were then transferred directly to a drop of glycerol on a glass slide for microscopic examination.

More intensive clearing is necessary for accurate and systematic tabulation of body pores and sensilla. All tissue was removed from within the integument by heating specimens in a 10% aqueous KOH solution at 80° to 100°C for 2 to 4 h. Rapid boiling should be avoided to prevent the integument from breaking apart. The ratio of KOH solution to specimens was about 50 cc per individual. The KOH digestion was repeated using fresh solution if precipitates or fatty substances remained within the integument. The concentration of KOH has been increased on occasion to 25% with satisfactory results. For ease in viewing during microscopic analysis, it is essential in preparing the specimen to digest all tissues and eliminate precipitates from within the integument.

Following digestion the empty, still intact, exoskeleton is prepared for staining by a rinse in distilled water for 1 to 2 min and transfer to 70% ethanol for 1 to 2 min. These rinses should be repeated if flocculent precipitates remain within the integument. Immersion for about 30 sec in a solution of 1% CBE dissolved in 70% ethanol stains specimens intensely. Staining is terminated by flooding the preparation with distilled water and transfer of the specimen through a brief rinse in water to a drop of glycerol placed on a glass microscope slide for examination. Stained specimens suspended in glycerol may be stored indefinitely in appropriate slide storage boxes.

Washing and staining were carried out under a stereomicroscope using 3-spot deep depression slides and with solutions changed with the aid of finely drawnout glass pipettes equipped with rubber bulbs. Sensilla are usually lost in this process, leaving the stained cuticle punctured by clear perforations. Glandular pores also appear as clear perforations permitting light to stream through, but differ in shape and appearance of the margin as described below (p. 973).

Length measurements were carried out with the aid of a stereomicroscope at 24× and 40× magnifications depending on the size of the species. The microscope was equipped with a mechanical stage and an eyepiece reticle bearing a ruled scale of 100 divisions. Total length (TL) was taken from the right lateral view in two steps: one measurement along an imaginary line extending from the anteriormost tip of the forehead to the dorsalmost juncture between prosome and urosome (Fleminger, 1967) and the second along an imaginary straight line from the dorsalmost juncture of prosome and urosome to the posteriormost point on the right furcal ramus omitting the setae.

Examination of specimens for perforation number and distribution was carried out with the aid of a compound microscope equipped with a mechanical stage at magnifications of 150× to 600×. A camera lucida was used in the preparation of drawings to approximate spatial arrangement of perforations in each form.

The outline drawing with perforations was reproduced by electrostatic duplicating machine for use on subsequent specimens of the species as a data recording form. Allowance was made for small variations in the distance between regularly occupied perforation sites; all missing and additional perforations were recorded on the form together with length measurements, sample, and specimen number. No attempt was made to estimate variability in the distance between adjacent perforations.

GENERAL OBSERVATIONS

Three general types of sensilla were found in *Eucalanus* (Figures 2, 3). They resemble relatively simple types found in other arthropods (e.g., see Snodgrass, 1935; Bullock and Horridge, 1965; Schneider, 1969) and are as follows:

1. Hair (trichodea) sensilla (Figure 2d); slender, elongated, uniformly attenuated, and unarmed; roughly 20 to 150μ in length and 1 to 5μ in diameter at the base; observed only on thoracic segments II to V.

2. Peg (basiconica) sensilla (Figure 2g); with pointed or rounded apex, ranging from 14 to 27μ in length, 1 to 3μ in diameter; they are widely distributed over the prosome and usually occur adjacent to the pore of an integumental gland.

3. Pit (coeloconica) sensilla (Figure 2i): shallow circular depressions in the integument, 3 to 6μ in diameter, the center raised in a nipple-like protuberance that stains intensively in CBE-lactic acid; they were observed in few species and only on the cephalon and anterior thoracic segments.

As a rule the sensilla are lost during the course of tissue digestion and staining. Perforations representing the sites of sensilla in prepared specimens appear under the light microscope as simple round openings. The innermost margin stains noticeably lighter than the surrounding integument. Large perforations ($\geq$ 4μ) from large hair sensilla may have a craterlike margin on the outer surface (Figure 2e). Under the light microscope the walls of the perforation may slope to form a larger elliptical outline on the inner surface of the integument. Perforations derived from pegs are simple and about 1 to 2μ across (Figure 2h). Perforations derived from pit sensilla appear as a pair of very small openings separated by a slender ridge (Figure 2j). One or more of the three types of sensilla were found on all segments of the cephalon and thorax. One aesthetask-like sensillum, usually weakly plumose, is present distoventrally on the furcal rami in all species. No other sensilla were observed on the urosome.

The other class of cuticular perforations are formed by the ducts of underlying integumental glands (Figure 2b). The glandular pore tends to vary from a semicircular to a slitlike opening of 4 to 7μ across the maximum dimension when viewed from above (Figure 2f-j). The margin stains as intensely as the surrounding cuticle and at least a section of the circumference turns inward toward the underlying hypodermis.

My use of the term pore in connection with integumental glands does not imply relationship to a different integumental feature, pore canals (Richards, 1951) discussed below.

Microscopic examination (300× to 600× magnification) of intact specimens, especially those belonging to the elongatus group (treated

with CBE-lactic acid), frequently confirmed the connection between the pore and a single, gland-like, spherical to ovoid sac, roughly 30 to 75μ across the maximum dimension (Figure 2b), and not unlike the glands noted in other copepods (Fahrenbach, 1962; Clarke et al., 1962; Park, 1966). Integumental glands may occur on all the segments of the body (Figure 3).

A notable feature of the perforations (both sensilla and gland duct types) is their relationship to formation of the integument. Resembling that described in other arthropods (Dennell, 1960), the exoskeleton in *Eucalanus* has been observed in the present study to consist of prisms apparently laid down over individual cells of the hypodermis. The prisms are joined by interprismatic septa presumably of secreted procuticle that stains darker with CBE than the prisms. The organ-forming and neural cell extensions pass between cells of the hypodermis. Hence passage of these features through the integument occurs in the interprismatic septa, a feature frequently observed in this study in all of the species. In specimens with well differentiated prisms, numerous minute perforations formed by the pore canals (~0.1 to 0.3μ) may be seen within each prism. As Dennell (1960, p. 461) states, perforations observed on the surface of the cuticle formed by integumental organs and pore canals cannot be confused; the latter are numerous, minute, and within the margins of individual prisms; the former are an order of magnitude larger and lie in the septa between prisms. Pore canals were not considered in the analysis of *Eucalanus* perforations.

LIMITATIONS

Failure to obtain total elimination of tissue and precipitates in the hot alkali treatment and insufficient staining were the commonest sources of difficulties in carrying out microscopic examination of the perforations. Specimens that had moulted shortly before fixation and species in which the exoskeleton is relatively flabby (e.g., species of the elongatus group) require greater care in staining and handling.

Occasionally, areas of perforation size fail to take up as much stain as the surrounding

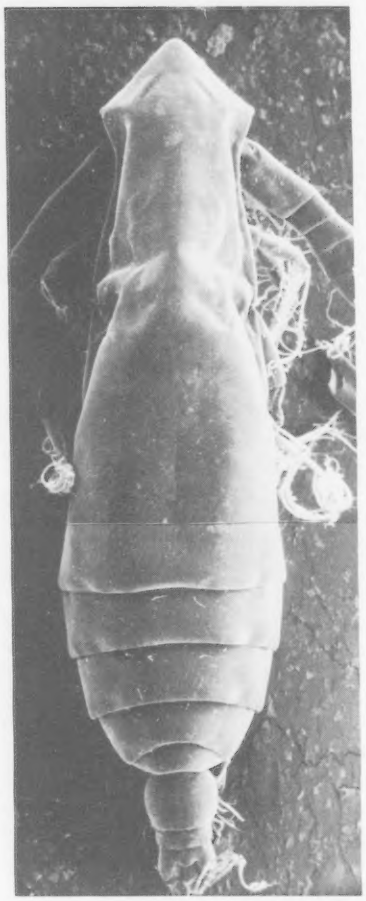
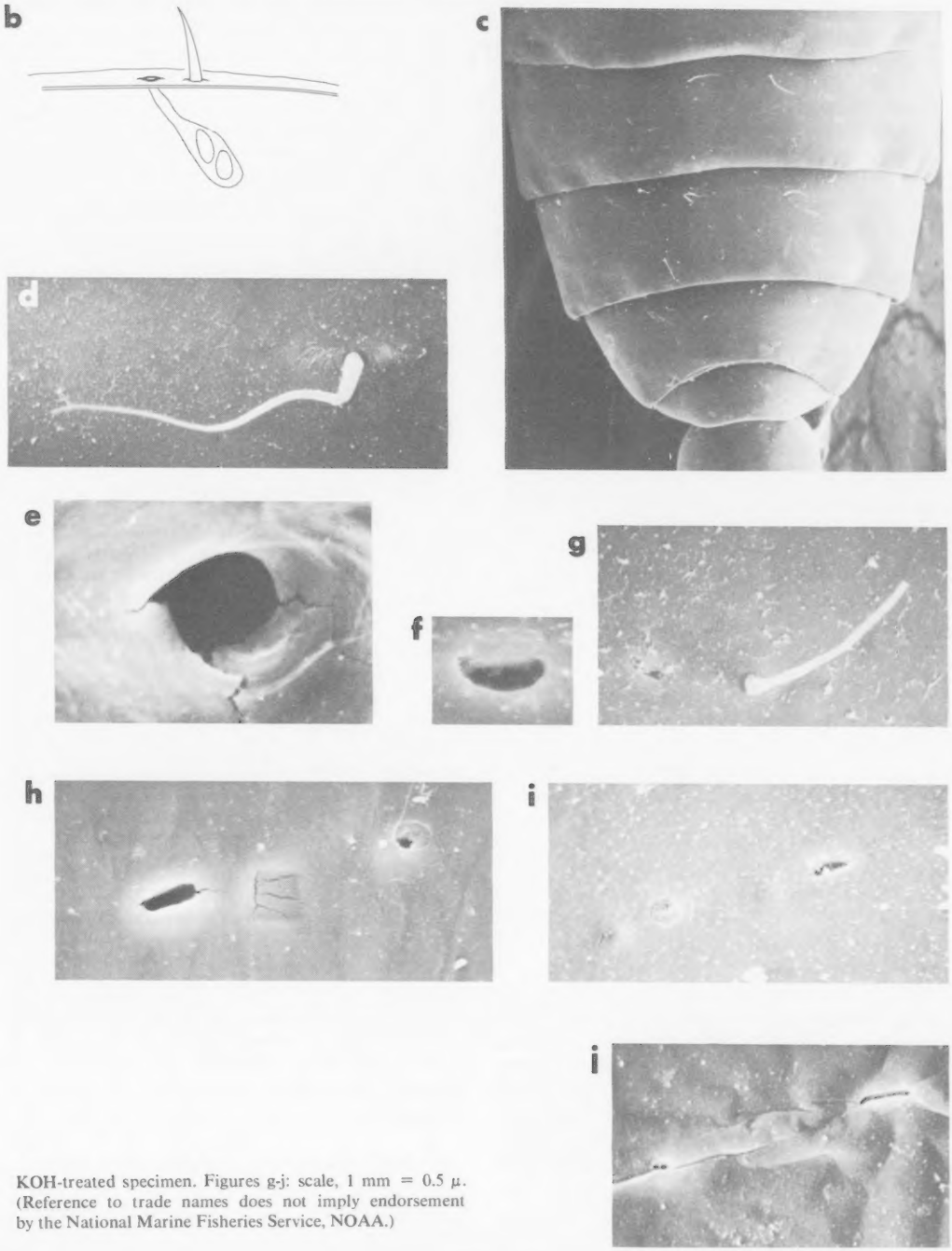


FIGURE 2.—Appearance of intact integumental organs and the perforations left by these organs in the integument of KOH-treated specimens of *Eucalanus subtenuis* (adult females). Specimens prepared for scanning electron microscope by Freon critical-point drying, vacuum coating with gold-palladium and examined with the aid of a Cambridge Stereoscan S.E.M. **a.** entire specimen in dorsal view; 1 mm $\cong$ 24.4 μ. **b.** schematic sectional view of typical combination of peg (basiconicum) sensillum and integumental gland with pore. **c.** thorax in dorsal view; 1 mm $\cong$ 8.5 μ. **d.** hair (trichodeum) sensillum; 1 mm = 1 μ. **e.** perforation in integument left by hair sensillum in KOH-treated specimen; 1 mm = 0.25 μ. **f.** pore of integumental gland; 1 mm = 0.25 μ. **g.** typical arrangement of peg sensillum (right) and pore (left). **h.** perforations in integument left by peg sensillum (right) and pore (left) in KOH-treated specimen. **i.** pit (coeloconicum) sensillum (left) and pore (right) of integumental gland. **j.** perforations in integument left by pit sensillum (left) and pore (right) in



KOH-treated specimen. Figures g-j: scale, 1 mm = 0.5 μ. (Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.)

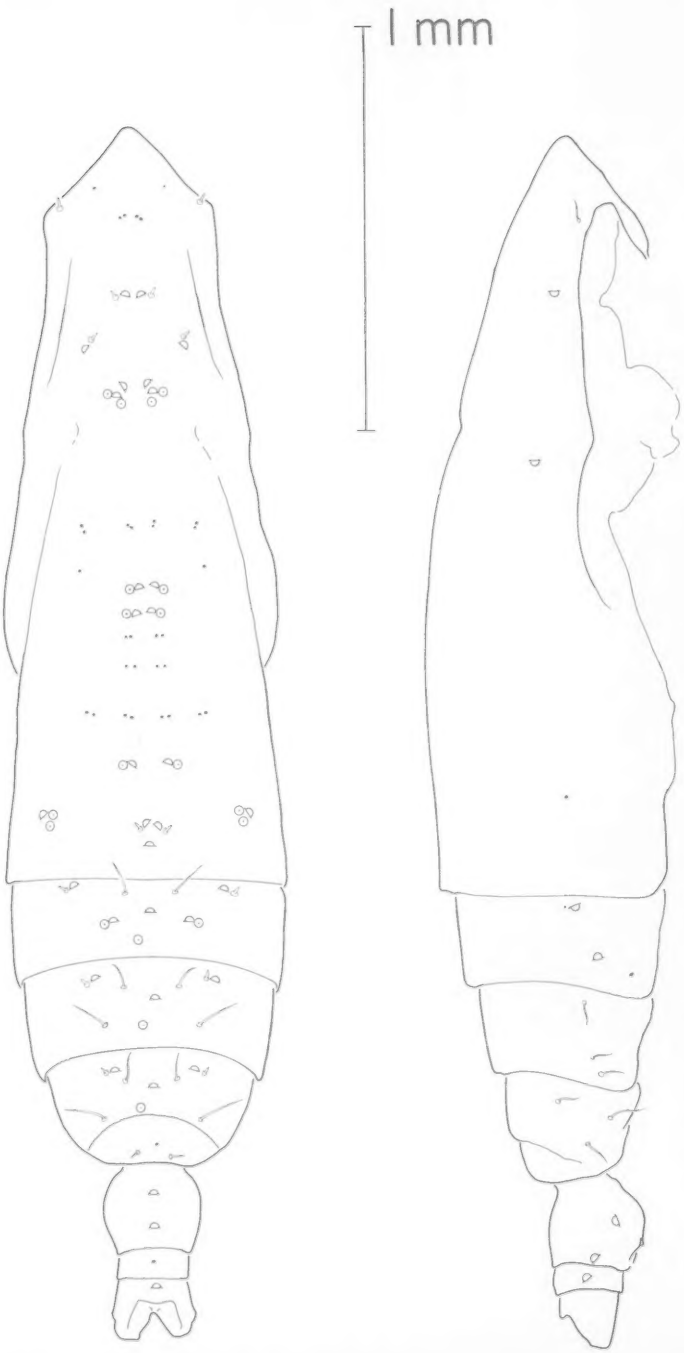


FIGURE 3.—Distribution of sensilla and pores of integumental glands in an adult female specimen of *E. subtenuis*; dorsal view on left, lateral view on right. Hair sensilla are shown as curving, attenuated, and varying in length; peg sensilla are short, straight and blunt; pit sensilla are shown as an open circle with a dot in the middle. Pore of integumental glands shown as a half circle. Solid dots represent perforation sites observed in specimen after KOH-CBE treatment and represent organs missed during microscopic examination of the specimen before digestion of tissues; intact specimen cleared in CBE-lactic acid solution for 24 h prior to examination. All organs shown enlarged and schematically, though position is based on records obtained from camera lucida drawings; microscopic examination carried out at magnifications of from 150x to 600x.

integument and appear as light spots that may be mistaken for perforations. Direct comparison with a true perforation is helpful to note the reduced intensity of illumination passing through the light spot. Light spots tend to occur in the vicinity of usual perforation sites found in the genus and may represent incomplete or arrested development of a gland or sensillum. Light spots were not recorded as perforations.

A number of perforations relatively difficult to observe were not examined systematically. They include the dorsal surface of the furcal rami and cephalolateral sites in the vicinity of the first and second maxillae and the maxilliped. The ventral surfaces of the prosome appear to have few perforations but were not examined systematically.

DISTRIBUTION OF INTEGUMENTAL ORGANS

In each species the three types of sensilla and pores of integumental glands maintain essentially constant topographic relationships in arrangement and number on both the dorsal and lateral surfaces of the body, as seen for instance in *subtenuis* (Figure 3). One notable pattern appearing in all of the species for example is the distribution of dorsal hair sensilla, two appearing on the second thoracic segment, four on the third, and four on the fourth, the hairs always being arranged in transverse symmetrical rows, two hairs in each row (Figure 3). Another type of persistent pattern is the regular occurrence of the peg sensillum adjacent to the pore of an integumental gland (Figure 2). The organs are distributed in bilaterally symmetrical patterns that exhibit serial homologies. Serial homology is indicated by the partial to complete repetition of patterns in adjacent segments. As is shown below in the account of the different species, the closer the general morphological similarities between individual pairs of species the more similar the overall perforation patterns.

Every morphological type of sensillum or gland pore occupies a topographically unique position, i.e., a designated site within the framework of the overall bilaterally symmetrical pattern. The designated sites appear in KOH-treated specimens as morpholigically distinctive perforations in the integument. Each body segment has a constant number of organs (Table 3) arranged in a distinctive pattern that is repeated with negligible variation within the series of specimens representing the species. Hence on an empirical basis the appearance of the same type of perforation in approximately the same topographic relationship in the series of specimens representing the species is compelling evidence that similarly positioned organs of the same type are homologous among individuals of the same species. That is, they appear to bear the morphogenetic relationships that are a primary basis for regarding the same cephalic or thoracic appendage among individuals of a population as being homologous. Thus the array of regularly appearing integumental organs (designated sites) among the individuals of the species is assumed to comprise a homologous set characteristic of the species.

Among the species of a species group, integumental organs appearing in topographically similar positions on the same body segment in all of the species are viewed as comprising a homologous set characteristic of the species group. The integumental organs common to the various species groups comprise the homologous set characterizing the genus. The implication of phylogenetic redundancies is seen in comparing perforation patterns among the species (see Figures 9, 11, 13, 15) presented below and in a segment-by-segment comparison of the number of regularly appearing sites in the species and species groups (see Table 3 and Figures 8, 9, 11, 13, 15).

In the case of a fused series of somites, i.e., a tagma such as the cephalosome, the patterns are arranged in accord with the sets of body appendages in the tagma. The number of homologous sites within the members of a species group is relatively high (cf. Figure 8 with Figures 9, 11, 13, 15) and the number of homologous sites within the genus (55) is remarkably high (Figure 6) considering that the species range from a low of 83 sites in *longiceps* to a high of 131 shared by *bungii* and *californicus* (Table 3).

TABLE 3.—Total number of lateral and dorsal perforation sites, by body and abdominal segments in ≥80% of *Eucalanus* specimens examined. Body segments indicated by corresponding appendages.

Genus & species	Anterior body segments								Midbody segments					Abdominal segments					Grand total
	A1	A2	Mnd	Mx1*	Mx2*	Mxp*	P1	Total	P2	P3	P4	P5	Total	Abd 1+2	Abd 3	Abd 4	Abd 5	Total	
Eucalanus:																			
Number of homologous sites in genus	8	6	4	4	2	4	1	29	5	6	6	2	19	2	2	—	1	5	53
subtenuis group:																			
subtenuis	12	6	10	10	4	4	17	63	14	18	15	3	51	6	2	1		9	122
mucronatus	8	6	6	6	4	4	9	43	12	14	13	3	42	6	2	1		9	94
crassus	8	6	8	6	—	4	5	37	11	13	13	3	40	4	2	1		7	84
longiceps	8	6	6	6	—	4	5	35	11	13	13	3	40	5	2	1		8	83
monachus	8	6	6	6	—	4	5	35	13	15	13	3	44	5	2	3		10	89
Number of homologous sites in group	8	6	6	6	—	4	5	35	11	13	13	3	40	4	2	1		7	82
pileatus group:																			
pileatus	8	6	6	8	—	4	5	37	11	14	14	3	42	5	2	3		10	89
subcrassus	8	6	6	10	4	4	9	47	15	18	14	3	50	7	4	1		12	109
dentatus	8	6	6	8	4	4	9	45	15	18	14	3	50	7	4	3		14	109
Number of homologous sites in group	8	6	6	8	—	4	5	37	11	14	14	3	42	5	2	1		8	87
elongatus group:																			
elongatus	10	6	4	6	2	8	7	43	7	10	10	4	31	8	4	4	1	17	91
hyalinus	12	6	8	6	10	16	9	67	9	11	10	4	34	7	4	4	1	16	117
inermis	14	6	8	4	6	12	11	61	7	10	9	3	29	4	2	—	3	9	99
bungii	12	6	6	4	12	16	15	71	13	14	12	4	43	8	4	4	1	17	131
californicus	12	6	6	4	12	16	15	71	13	14	12	4	43	8	4	4	1	17	131
Number of homologous sites in group	10	6	4	4	2	8	7	41	5	7	9	3	24	4	2	—	1	7	72
attenuatus group:																			
attenuatus	12	6	4	6	4	12	11	55	13	16	16	6	51	8	2	7		17	123
sewelli sp.n.	12	6	4	6	4	12	11	55	13	12	12	6	43	6	2	5		13	111
parki sp.n.	12	6	4	6	4	12	11	55	13	12	12	4	41	7	3	5		15	111
langae sp.n.	12	6	4	6	4	12	11	55	13	12	12	4	41	8	3	10		21	117
Number of homologous sites in group	12	6	4	6	4	12	11	55	13	12	12	4	41	6	2	3		11	107

*Lateral perforation not counted.

VARIATION AT DESIGNATED SITES

As described above designated sites are those topographic positions on each segment occupied by an integumental organ of a morphologically specified type that occur within the context of a relatively fixed pattern on each segment. The pattern on each segment is primarily characteristic of the species and includes elements characteristic of the species group and of the genus as well.

No variation was observed in the morphological nature of the organ occupying the designated site during occasional examination of randomly selected intact specimens or in the characteristic type of perforation observed at the site in the sample of the species that was examined. Small differences in the relative distance between adjacent sites within the pattern of a segment were observed frequently. They are negligible, however, with respect to influencing the accuracy of recording details for each specimen. Replicate counts of the same specimens taken on subsequent days usually yielded similar results; the few departures from zero variation ranged from 1 to 3%. Spatial variation was not examined closely. Better understanding of its significance should be developed, as it probably reflects individual morphogenetic and possibly genetic differences.

Quantitative variation in terms of failure to find a perforation at a designated site or finding a perforation in excess of the regular number characterizing the segment (Table 3) is remarkably low. To the extent that spatial variability does occur, it may be argued that the basic

scoring of individual perforations as representing particular sites contains an element of judgment on the part of the observer.

Constant repetition of pattern (per body segment per species) in the distribution of perforations (see Figures 9, 11, 13, 15) and the small amount of variation in the total number of perforations observed in each species (Table 4) indicate that personal judgment by an experienced observer introduces negligible bias. The range about the mean number of perforations per species (Table 4) does not exceed 10% with exception of *subtenuis*, a special case actually representing three allopatric populations occupying separate regions of the world's tropical belt. Indeed, perusal of Table 4 indicates that quantitative variation is not a simple function of either sample size or total number of perforations.

With respect to presenting variation scored for each species, the frequency of a perforation appearing at each designated site is presented symbolically in three categories: sites occupied in all specimens, sites represented in 80 to 99% of the specimens, and sites represented in 10 to 79% of the specimens (see Figures 9, 11, 13, 15).

TABLE 4.—Number of localities, size of pooled sample, and number of observed perforations in species of *Eucalanus*.

Species	Localities	Specimens	Perforations Range	$\bar{x}$	s
subtenuis group:					
subtenuis					
Atlantic Ocean	15	50	125-141	134.8	3.2598
Indian Ocean	10	24	119-139	130.0	4.9111
Pacific Ocean	10	36	114-135	123.6	4.9750
mucronatus	6	20	86-91	89.4	1.5355
crassus	4	11	83-85	84.0	0.4713
longiceps	4	12	79-83	82.7	1.1572
monachus	5	17	87-91	88.8	0.8106
pileatus group:					
pileatus	8	21	85-94	90.5	2.0384
subcrassus	9	34	109-117	110.1	2.4722
dentatus	5	24	109-115	111.5	1.3313
elongatus group:					
elongatus	11	19	90-101	94.9	3.3154
hyalinus	14	25	109-121	114.8	3.2490
inermis	7	16	94-106	99.7	2.7500
bungii	5	15	127-133	130.1	1.8086
californicus	6	23	125-135	131.2	2.1829
attenuatus group:					
attenuatus	16	26	117-126	122.0	2.0703
sewelli sp.n	24	43	107-113	110.3	1.2070
parki sp.n.	5	18	109-114	111.5	1.3323
langae sp.n.	7	14	115-121	117.6	1.7388

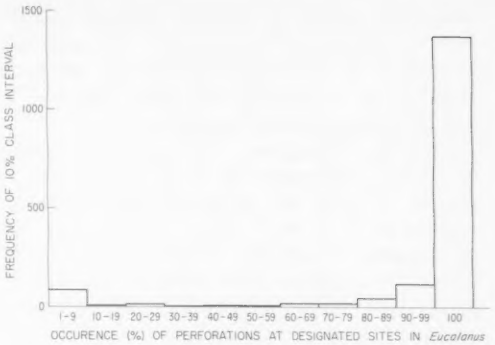


FIGURE 4.—Frequency of occurrence of perforations at designated sites on the dorsal and right lateral integument of *Eucalanus*. The frequencies found in each species are grouped in class intervals of 10% and each class is summed for all species. Each designated site represents the occurrence of a particular type of integumental organ appearing in a KOH-treated specimen as a distinctive perforation in the integument and occupying a topographically unique place within the framework of the overall bilaterally symmetrical pattern found in the species. For purposes of this graph the appearance of such a distinctively placed perforation in only one specimen of the pooled sample for the species is sufficient to include it among the number of designated sites found in the species. Graph based on examination of 448 adult female specimens representing 17 species that yielded a total of 1,709 designated sites as defined above.

Sites found in less than 10% of the sample have been omitted. A general summary of the variability at each site is presented in Figure 4. Roughly 80% of the sites were represented by a perforation in every specimen. In 10% of the sites a perforation was observed in 80 to 99% of the sample. The remaining 10% of the sites were occupied at lower frequencies, but this category includes a number of sites that show remarkable patterns of geographical variation in *subtenuis* that are discussed below.

Designated sites do not vary with respect to type of organ they represent, but one class of variation in topographic relationship is noteworthy. As mentioned above, peg sensilla regularly occur adjacent to the pore of an integumental gland. The peg and pore pairing often varied with respect to the position of the two relative to the orientation of the segment. The peg tends to be lateral to the pore, but this may be completely reversed or appear at any intermediate stage about a 360° arc. As a pair, how-

ever, they occupy a discrete position relative to the remainder of the sites on the segment. This class of variation also deserves increased attention as a potential fine scale indicator of intrapopulation genetic variation.

Thus for application of integumental organs to copepod systematics at or above the rank of species, variation encountered during this study appears to be of no consequence. Moreover, the intraspecific variability observed may on the basis of experience with *subtenuis* provide a dependable, measurable source for studying population homogeneity and gene flow.

PERFORATION SITES IN THE GENUS

Intra- and interspecific comparisons of perforation number and arrangement are facilitated by compelling evidence that sites similar in location and associated organ (i.e., gland pore or sensilla type) within and between species are homologous. Tables 3 and 4 and figures of individual species summarize the evidence that in general perforation number and topographic arrangement are essentially constant and characteristic for each species. Further, all of the available observations indicate that the type of organ found at any particular perforation site is also constant.

As shown below, constant differences in numbers and arrangement of perforations between the morphologically more similar species are small. Quantitative and topographic differences are correspondingly greater between species that are more dissimilar morphologically (e.g., Figures 9, 11, 13, 15). However, the total number of perforation sites in the genus appears to be about two times the number found in any one species (Figure 5).

To construct Figure 5 an assessment of the extent of interspecific homology in sensilla and pores of *Eucalanus* was obtained by rigorous comparison of all the species segment by segment. The tabulation was restricted to designated sites, i.e., those occurring in 10% or more of the specimens of each species. As described above, sites are judged to be homologous if they occur on the same segment in the same general position relative to the pattern characteristic of the segment and represent the same kind of organ (gland pore or type of sensilla). The place of insertion of the segment's paired appendages and the topographic position relative to the other sensilla and gland pores of the segment aid in locating perforation sites. Overlaps of camera lucida sketches were also helpful when allowance was made for relative and absolute differences in size. Allowance was also made for small-scale variation of one or two perforations relative to another one or a set as in peg and pore pairings; small differences in the spacing between adjacent sites and rotation of one site relative to another was observed frequently within the general pattern arrangement of individual species.

The analysis reveals 163 different dorsal pore and sensilla sites and 30 lateral sites on each side of the body. The total number of different sites within the genus (223) is less than twice that of the species with the highest individual score (Table 3). Thus most sites in the genus appear to be common to many of the species and an appreciable number is common to all (Figure 6).

Examination of small numbers of copepodid stages IV and V, adult males of all species and a few specimens of copepodid stage III indicated conformity of each to the pattern characteristic of the species, except for segments that undergo sexual modifications in the process of maturation.

PERFORATION NUMBERS AND PATTERNS AMONG THE SPECIES GROUPS

Interspecific comparison of the perforations observed in *Eucalanus* is, as already mentioned above, greatly simplified by the not unreasonable assumptions that repetitious similarities in pattern are dependent upon and a direct reflection of genetic similarities. With this as a working hypothesis, reducing and assimilating the distribution of perforation sites was enhanced by assembling similarities among the different species and by using for comparisons all other constant topographic features of the integument.

All the species have in common 37 tergal sites, best seen in dorsal view and 9 pleural sites

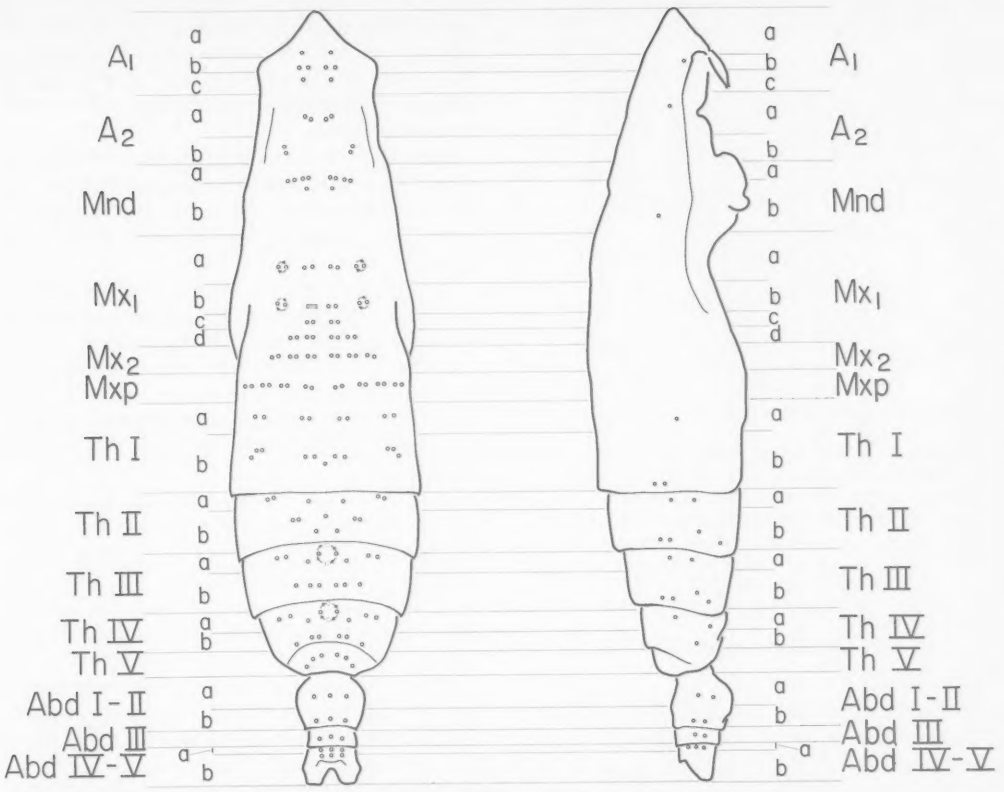


FIGURE 5.—Schematic presentation of all designated sites observed in adult female *Eucalanus*. Open-ended system for designating individual sites provided by abbreviations of appendages or abdominal segments together with row (a, b, . . .) and in dorsal view number to left or right of midline, or in lateral view number in dorsal to ventral order.

Cephalosome in *Eucalanus* contains the cephalon extending from the first antennae (A1) to the second maxillae (Mx2), the maxillipedal somite (Mxp = Th0) and the first pedigerous somite (ThI). Thoracic segments ThII, ThIII, ThIV bearing swimming legs 2, 3, and 4 are separate from one another, but ThV lacking a pair of swimming legs in the female is partially fused to ThIV. In the female abdomen the first two somites are fused (Abd.I-II) during maturation of the genital segment. Abd.III is separate and Abd.IV is separate in the elongatus species group but fused to Abd.V in the other three species groups. The furcal rami are fused to Abd.V in all the species.

on each side, best seen in lateral view (Figure 6). Tergal sites on the cephalosome are pores and peg sensilla; on ThII to ThV, all but two (ThII-mb and Abd.IV-V-m) are hair sensilla; the two exceptions are pores. The pleural sites of the cephalosome appear to include both pores and peg sensilla. Pleural sites on ThII to ThIV are hair sensilla and those of the urosome are pores.

Within the genus four groupings may be distinguished by virtue of additional perforations that appear in common only among the species comprising each group (Figure 8). Additional support for these groupings may be found in other morphological characters of taxonomic value in *Eucalanus* such as segmentation of the abdomen and the shape of the seminal receptacles in females (Figure 1), fifth legs of adult males, and various details in the appearance of the cephalosome. The groupings and their complement of species and geographical forms are listed in Table 1.

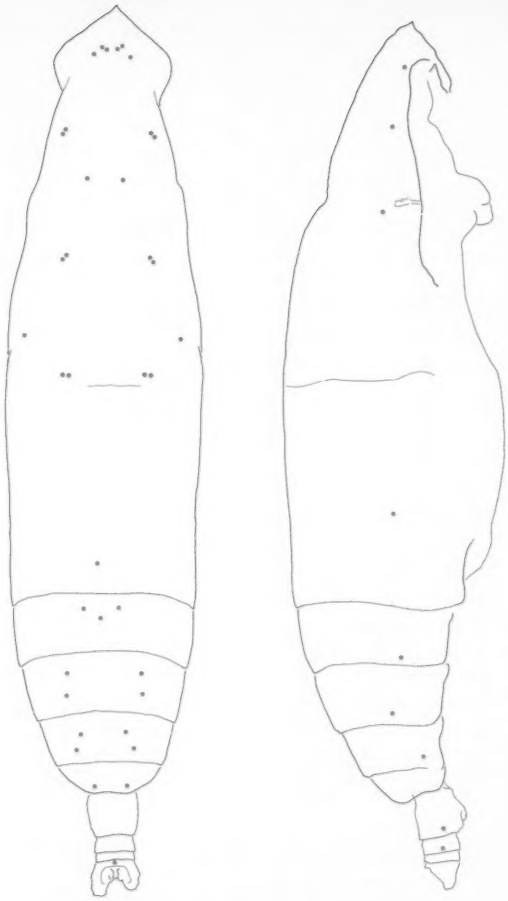


FIGURE 6.—Designated sites (represented by a dot) occurring at frequencies of ⩾80% within the pattern of each species and present in every species of the genus *Eucalanus*. Dorsal view on left, lateral view on right; outline of organism based on *elongatus* used solely as vehicle to show topographic relationships of sites.

The Subtenuis Group

Sites distinguishing the subtenuis group (Figure 8c) appear on various portions of the cephalosome and thorax. On the cephalon the mandibular somite bears two pairs of tergal sites. ThI shows only three sites arranged in a transverse row. ThIII and ThIV are similar, both being characterized by bilateral tergal pairs lying outside and anterior to the quadrangle of hair sensilla and a single medial site slightly posterior to the anterior hair sensilla. The subtenuis group contains five generally accepted species that occur typically in eutrophic oceanic waters.

Sites in *E. crassus* (Figure 9a) are identical with the pattern of the species group except that the perforations of row a on the mandibular somite are increased to two pairs (Mnd T-a-*l*1, *l*2 and r1, r2).

E. longiceps differs from the group pattern solely by the presence of a single mediodorsal site on the genital segment (Figure 9b).

E. monachus (Figure 9c) differs from *longiceps* in two features: the occurrence of a transverse row of three tergal sites across Abd.IV-V and three pleural sites on ThII, ThIII, and ThIV.

E. mucronatus (Figure 9d) shows a small increase in the number of sites. On the cephalosome up to six pairs of tergal sites may appear in addition to the group number between the somite of the second maxilla and the maxillipedal somite. ThI shows an additional tergal pair on either side of the middorsal site. ThII and ThIII have an additional site in the posterior row (ThII T-b-*l*1 and ThIII T-b-*l*1) to the left, but the symmetrical homologue to the right of the middorsal axis is absent. On the abdomen the genital segment has two middorsal sites and Abd.III may have one.

E. subtenuis (Figure 9e) has the largest number of regular perforation sites in the genus. Dorsally, in addition to the species group number, two more pairs appear in the somite of the second antenna, up to eight more pairs between the somites of the first and second maxillae, four more pairs on the maxillipedal somite, four more pairs on ThI, and two more pairs on ThII. ThII and ThIII have a single asymmetrical tergal site (pore) within the quadrangle formed by the hair sensilla as in *mucronatus*. Laterally, ThII and ThIII both show one or more pairs on either side.

Within the group, *subtenuis* shows the largest number of perforations (Figure 10) and the most extensive geographical distribution relative to areal extent and sympatry (unpublished). Differences between *subtenuis* and its closest cognate, *mucronatus*, are concentrated in the

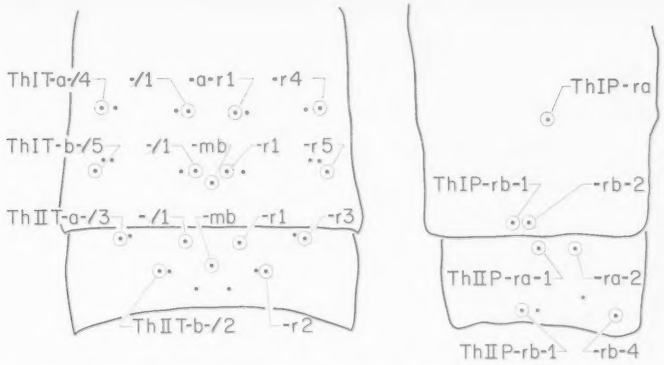


FIGURE 7.—Scheme for codifying designated sites in *Eucalanus*. Left: dorsal view of posterior portion of cephalosome and thoracic segment 2. Right: lateral view of same.

First unit of code for referring to a designated site is reference to the somite, using the appropriate appendage in the case of the cephalosome or the body segment (ThII, ThIII, . . ., Abd.I-II, Abd.III, . . .). Second unit indicates whether it is dorsal, i.e., tergal (T), or lateral, i.e., pleural (P). Tergal sets are grouped in transverse rows. Thus, perforations are designated as being on the right (r) or left (l) of the mid-sagittal plane and are numbered from the medialmost to the lateralmost (1, 2, . . .). Transverse rows are lettered in an anterior-to-posterior sequence (a, b, . . .). Perforations falling on the midsagittal plane are termed medial (m) and lettered in an anterior-to-posterior sequence (a, b, . . .).

Both right (r) and left (l) lateral, i.e., pleural (P), sets are numbered in a dorsal-to-ventral sequence (1, 2, . . .). For convenience anterior-to-posterior division into rows is utilized following the corresponding set of tergal sites and are also lettered in an anterior-to-posterior sequence.

Various sites in dorsal and lateral views in the figures are codified according to the scheme proposed above.

the tagma also showing the most extensive geographical variation. Geographical variation in *subtenuis* distinguishing the Indian, Atlantic, and East Pacific populations is discussed below (p. 999). The other four species fall within a narrow overlapping range (>80 to <95 perforations). Differences in number and arrangement especially in the genital segment characterize *crassus* and *mucronatus*, the two species overlapping geographically in the Indian and West Pacific Oceans. Differences in number and pattern also involving the genital segment distinguish *crassus* and *monachus* which co-occur in the Atlantic Ocean. *E. crassus* also differs from *longiceps*, a temperate species of the Southern Hemisphere, and from *subtenuis* in the sites on the genital segment.

The Pileatus Group

The pileatus group (Figure 8d) consists of three sibling species that are only weakly differentiated in general appearance from that of the subtenuis group. The pileatus group also strongly resembles the subtenuis group in perforation pattern, the primary differences being in a small increase in the number of middorsal sites on the thoracic segments. One additional pair occurs on the somite of the first maxilla, and single anterior middorsal sites are found on ThIII and ThIV. Three tergal sites may appear on the genital segment, but the posterior two of the three sites are irregular in occurrence in *pileatus;* therefore, at the species group level, the genital segment is best characterized by a single middorsal site.

Among the individual species *E. pileatus* is essentially undifferentiated from the pattern in the species group (Figure 11a). It lacks tergal sites on the somite of the second maxilla and on Abd. III, although it has three tergal sites across Abd.IV-V. It also lacks posterodorsal pleural sites on ThI, ThII, and ThIII. The genital segment may have one or two posterotergal sites in addition to the regular middorsal site.

E. dentatus and *subcrassus* share a number of features that separate them from *pileatus*, namely two tergal pairs of sites on the somite of the

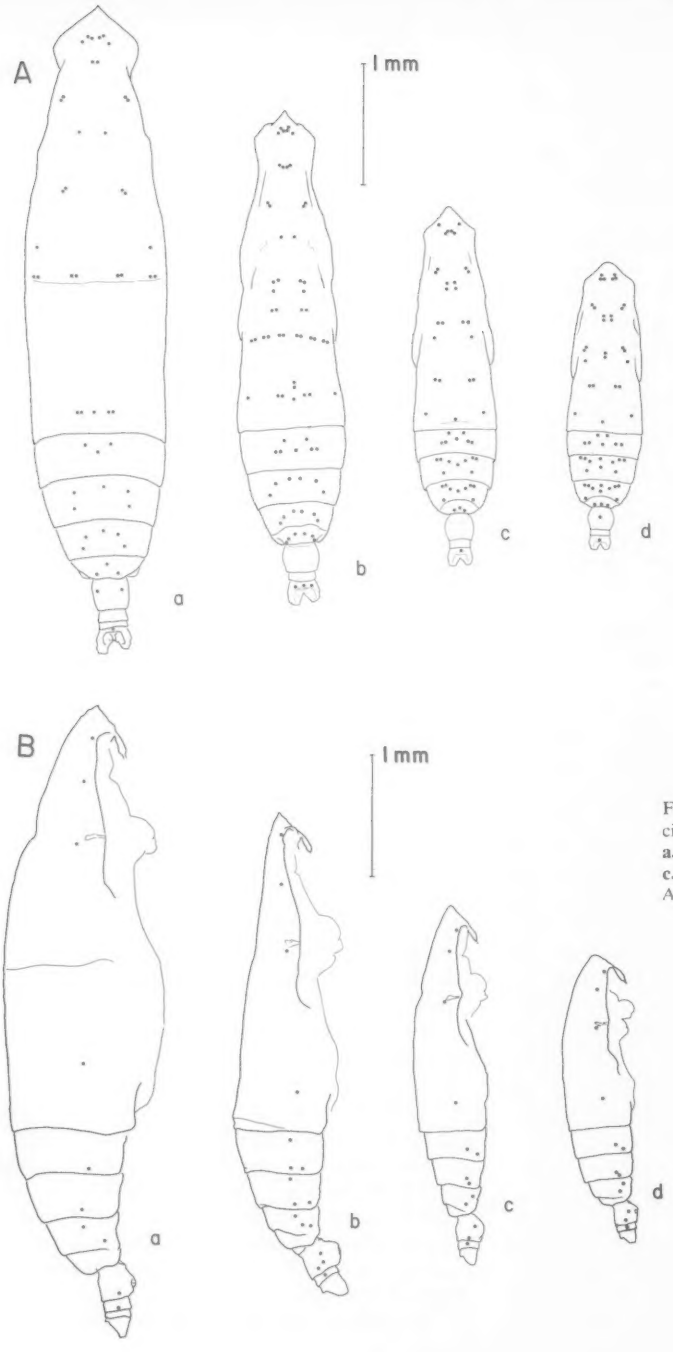


FIGURE 8.—Sites common to each species group of *Eucalanus*. From the left, **a.** elongatus group, **b.** attenuatus group, **c.** subtenuis group, **d.** pileatus group. A, dorsal view. B, right lateral view.

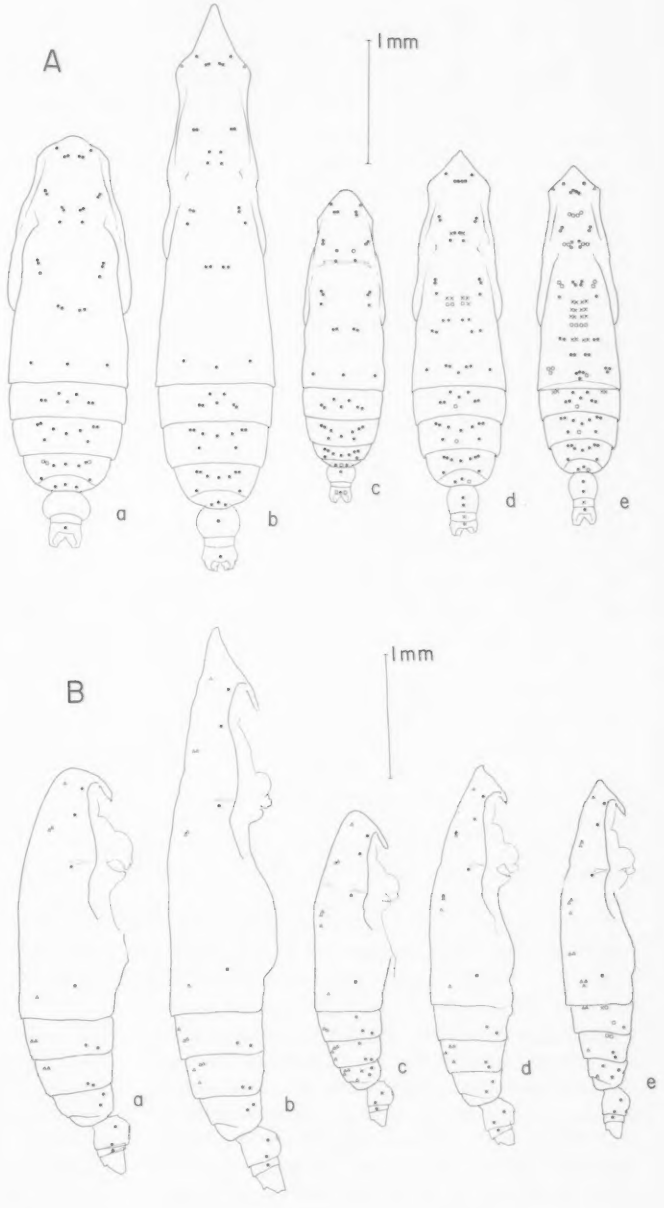


FIGURE 9.—Species of the subtenuis group of *Eucalanus:* **a.** *crassus,* **b.** *longiceps,* **c.** *monachus,* **d.** *mucronatus,* **e.** *subtenuis.* Dots represent sites occurring at a frequency of 100% in the pooled sample of the species; open circles are sites appearing in 80 to 99% of the pooled sample; crosses are sites occupied in from 10 to 79% of the pooled sample. Open triangles are sites also visible in lateral view but assigned to tergal sets. A, dorsal view. B, lateral view. All figures of adult females made with the aid of a camera lucida.

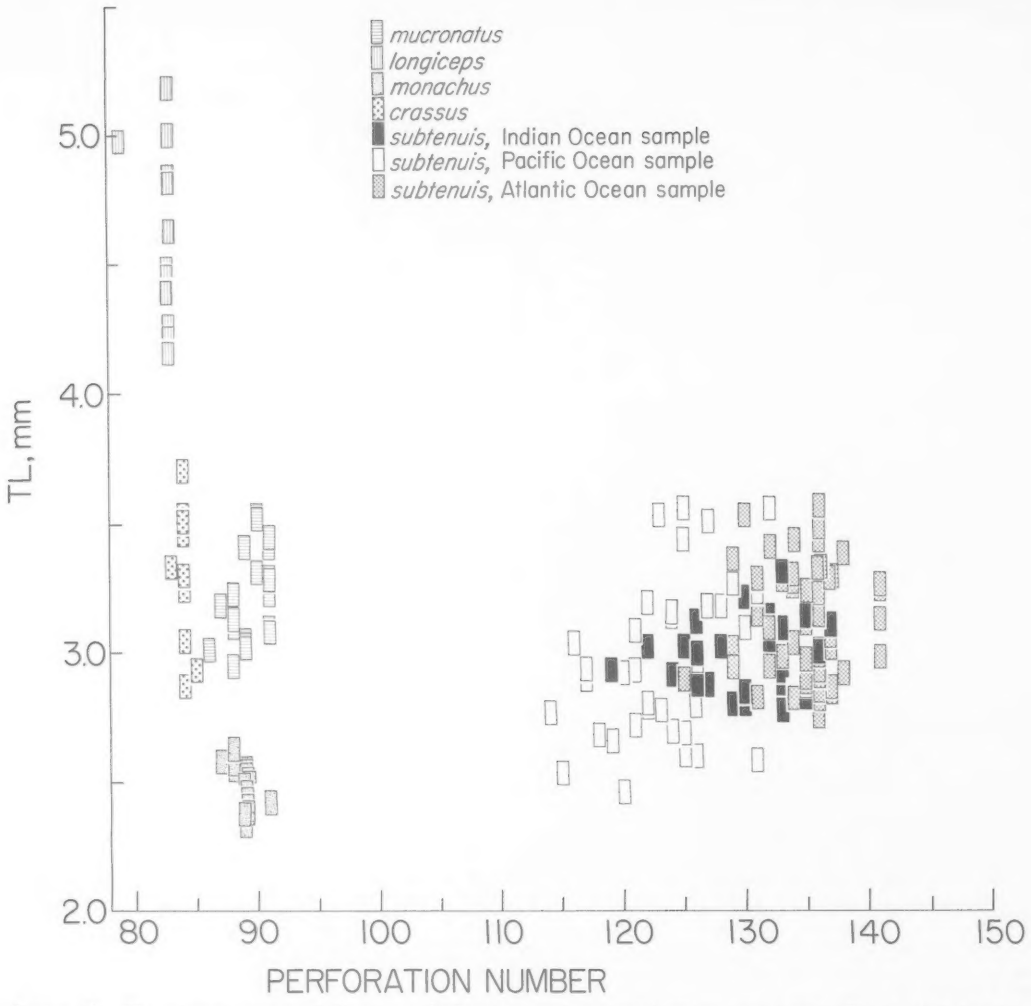


FIGURE 10.—The subtenuis group of *Eucalanus*. Perforation number plotted against total length (TL) in adult females comprising the pooled samples.

second maxilla, three tergal sites regularly on the genital segment, two or more tergal sites on Abd.III, and, laterally, a pair of posterodorsal pleural sites on each side of segments ThI, ThII, and ThIII. *E. dentatus* (Figure 11b) shows, in addition, three tergal sites across Abd.IV-V while *subcrassus* (Figure 11c) has a single middorsal site on Abd.IV-V.

As in the subtenuis group the species with the most extensive geographical range, the circumglobal *pileatus*, shows the most distinctive number of perforations within the species group (Figure 12). Differences between *subcrassus*, a broadly neritic species of the Indian and Pacific Oceans, and *dentatus*, a coastal species of Austral-Asian seas, are limited to arrangement, the number of perforations shown by the pooled samples of the two species being equal.

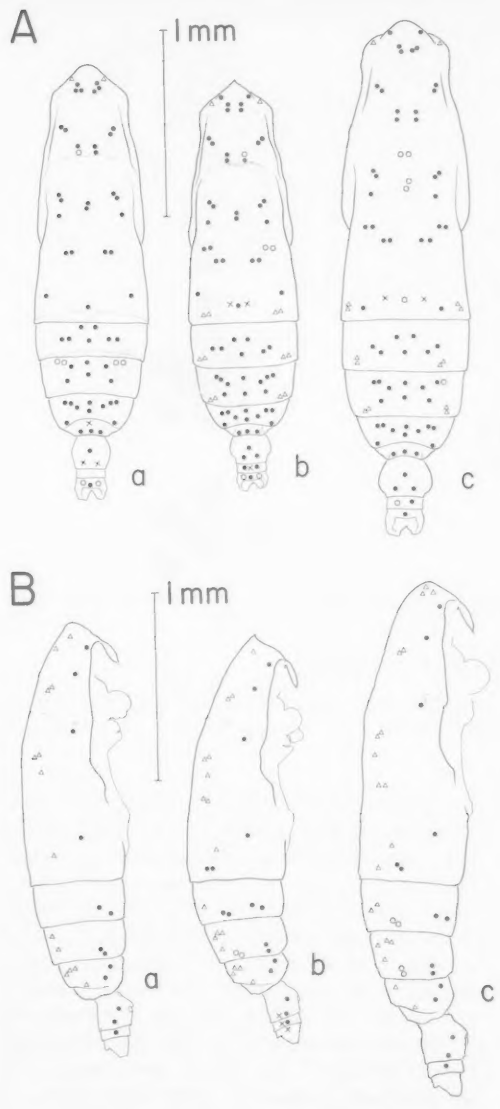


FIGURE 11.—Species of the pileatus group of *Eucalanus*: **a.** *pileatus*, **b.** *dentatus*, **c.** *subcrassus*. Dots represent sites occurring at a frequency of 100% in the pooled sample of the species; open circles are sites appearing in 80 to 99% of the pooled sample; crosses are sites occupied in from 10 to 79% of the pooled sample. Open triangles are sites also visible in lateral view but assigned to tergal sets. Dorsal view above, lateral view below. All figures of adult females made with the aid of a camera lucida.

The Elongatus Group

Species of the elongatus group are characterized by 1 pleural and 23 tergal sites in addition to the 37 and 9, respectively, present in the genus (Figure 8a). The increase represents the sum of one pair in the forehead (A2T-a-*l*1 and r1), two pairs on the maxillipedal somite (MxpT-*l*3, *l*4 and r3, r4), two pairs on the first free thoracic segment (ThIT-*l*1, *l*2 and r1, r2), one medial site each on ThIII, ThIV, and ThV, two dorsal sites on the genital segment, and one additional pleural site on each side of ThIV.

E. inermis (Figure 13a) is distinguished in dorsal view by the following tergal sites: a set of eight on the A1 somite, five on ThIV, three on ThV, two on the genital segment, none on Abd.-III and Abd.IV, and three on Abd.V. In lateral view diagnostic pleural sites on either side include one on the genital segment and none on Abd.IV.

E. elongatus (Figure 13b) differs from each of the other species in the group in a number of details but only the two anterior tergal sites on the second antennal somite (A2T-a-*l*1 and *r*1 and the tendency for more than two sites on Abd.III and Abd.IV are uniformly diagnostic within the group.

E. hyalinus (Figure 13c). Single tergal sites on ThI (ThIT-a-*l*1 and r1) and the three tergal sites on the genital segment distinguish *hyalinus* from the other species of the group.

E. californicus (Figure 13d). Sites that distinguish *californicus* from the preceding species are the pair middorsal on the somite of the second maxilla, the pair on the first free thoracic segment (ThIIT-a-*l*1, *l*2 and r1, r2), the pair flanking the median site on ThII (ThIIT-b-*l*1, *l*2 and r1, r2), and in lateral view the three pleural sites on either side of ThIV. No consistent difference in number or in arrangement of perforation sites was found that distinguishes *californicus* from *bungii*. Both species are morphologically distinctive in other respects (e.g., setation of the mandibular basis) and share a common boundary across the North Pacific, *californicus* occupying the temperate zone and *bungii* occurring to the north, without any apparent evidence of intergradation or hybridization.

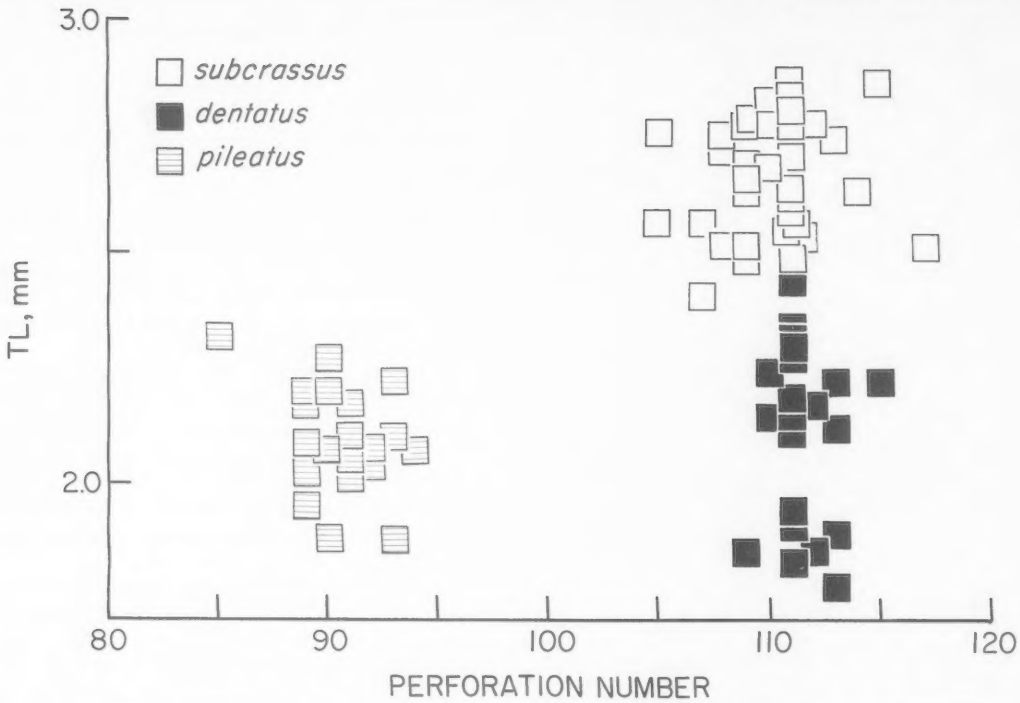


FIGURE 12.—The pileatus group of *Eucalanus*. Perforation number plotted against total length (TL) in adult females comprising the pooled samples.

As in the two preceding species groups a relationship between distinctiveness in overall number of perforations and geographical distribution is shown by the elongatus group (Figure 14). The only circumglobal species of the group, *hyalinus*, occupies a distinctive position with respect to perforation number. The two species to the left, *inermis* and *elongatus*, are geographically isolated from one another and the two species to the right, *bungii* and *californicus*, are biogeographically separated from one another. The distribution of *hyalinus* in contrast brings reproductively ripe individuals into contact with all of the other species except *bungii* (unpublished data).

The Attenuatus Group

Members of the attenuatus group have in common 38 tergal and 8 pleural sites added to the primary generic number (Figure 8b). The increase is widely dispersed about the body being found anteriorly on the second antennal somite (A2T-a-*l*1, *l*2 and r1, r2), the somite of the second maxilla (Mx2T-*l*1, *l*2 and r1, r2) and on the maxillipedal somite, where six pairs occur, two pairs more than in the elongatus group. Adding to the characterization are the anterior middorsal pair of ThI, the six symmetrically arranged tergal sites of ThV and the three tergal sites of Abd.IV-V. In lateral view pleural sites are also more numerous, three pleural sites on each side being found on ThII, ThIII, ThIV, and on the genital segment. Every segment except Abd.III bears more sites than the number characterizing the genus, and the group total of 109 sites is the largest among the four groups of species in *Eucalanus*.

Four discrete populations of *attenuatus* s.l. emerge from the present study. They are mor-

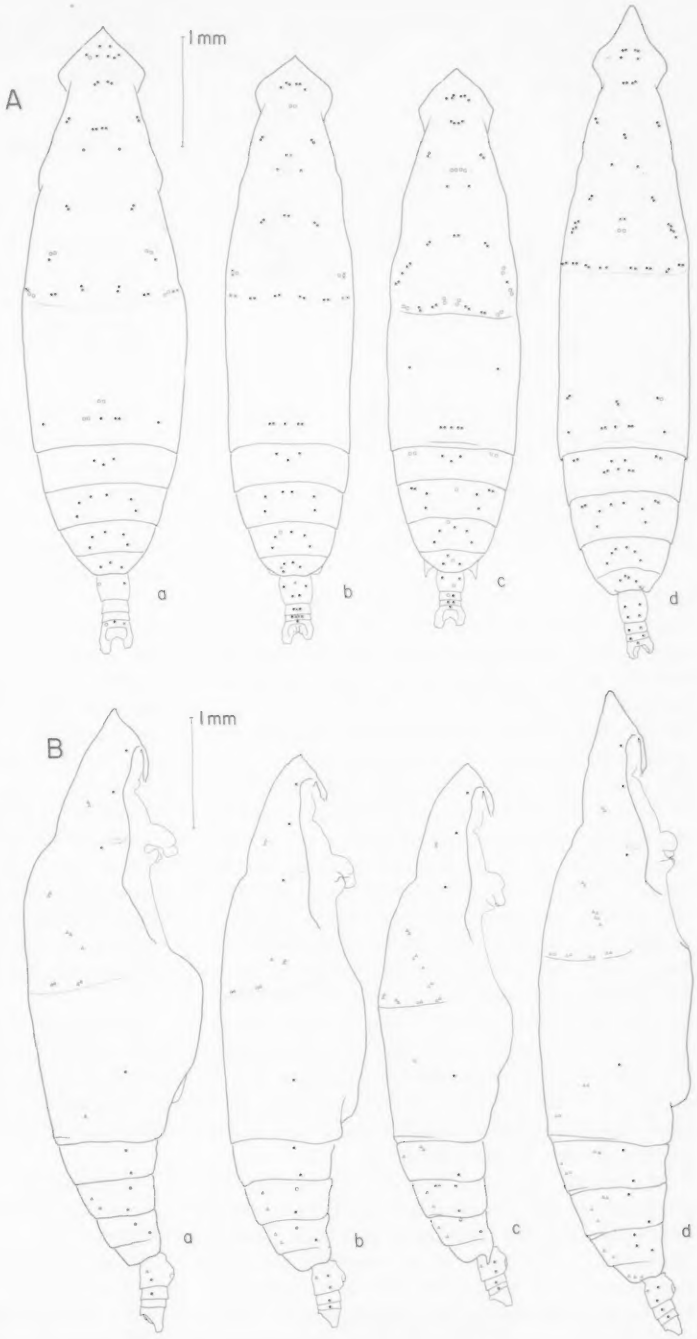


FIGURE 13.—Species of the elongatus group of *Eucalanus:* **a.** *inermis*, **b.** *elongatus*, **c.** *hyalinus*, **d.** *californicus*. Dots represent sites occurring at a frequency of 100% in the pooled sample of the species; open circles are sites appearing in 80 to 99% of the pooled sample; crosses are sites occupied in from 10 to 79% of the pooled sample. Open triangles are sites also visible in lateral view but assigned to tergal sets. Dorsal view above, lateral view below. All figures of adult females made with the aid of a camera lucida.

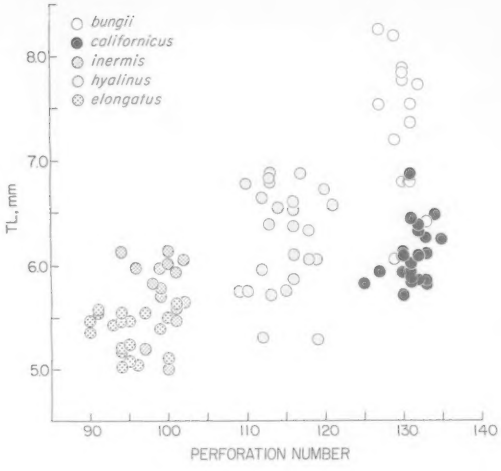


FIGURE 14.—The elongatus group of *Eucalanus*. Perforation number plotted against total length (TL) in adult females comprising the pooled samples.

phologically distinguished primarily by the number and arrangement of integumental organs and biogeographically by inferred distributions derived from the very different sets of geographical localities available for each form. In this regard it is important to stress that the sampling localities were chosen to represent the geographical extent of each population from hundreds of localities of *attenuatus* s.l. obtained during the course of global studies on several calanoid genera. In the case of the two unusually large species, *parki* and *langae*, the geographical records represent all that are on hand. A major factor favoring separation of this complex into four distinct species is the pattern seen in the preceding three species groups and repeated in the attenuatus group. That is, the species with the broadest geographical range also shows the most distinctive number or arrangement of sites, especially on the genital segment, and that related allopatric species may show little or no difference in these features.

In each instance the diagnosis is based on the adult female and stresses those designated sites characterizing the species within the group. Thus despite the more formal presentation and the addition of nonperforation data essential to describe each species the information on number and arrangement of designated sites is readily available within the diagnosis for each species.

Eucalanus attenuatus (Dana, 1849), *sensu stricto*

(Figures 1q, 15d, 18a, g, j, k, n, q)

E. attenuatus Dana, 1849, p. 18; 1853, p. 1080, Pl. 75, Figs. 2a-d; Vervoort, 1946, p. 95-103 (pars), Figs. 7a-c.

E. pseudattenuatus Sewell, 1947, p. 39, Test fig. 7A. NEW SYNONYMY.

Diagnosis: Adult female: Characterized by having the largest number of designated sites among the species of the attenuatus group (Figures 15d, 16; Tables 3, 4). Sites in addition to those of the species group include two pairs of tergal sites on ThIII (ThIIIT-b-*l*1, *l*2 and r1, r2), two similar tergal pairs on ThIV, two tergal sites on the genital segment, a single transverse row of three tergal sites on Abd.IV-V and, laterally, three pleural sites on either side of Abd.IV-V (Figure 15d). Length of triangular forehead extending beyond the lateral lobes overlying the first antennae usually shorter than width at origin, apex acute in lateral view and not curving ventrad (Figure 15d). Mandibular basis with two setae.

Adult male: Thoracic tergal sites as in female. Abd.II with two tergal sites (Figure 18j). Mandibular basis with two setae. Forehead weakly produced beyond base of rostrum, apex broadly rounded in dorsal and lateral views (Figure 18g, k).

Additional description: Female lacking fifth pair of legs, abdomen with three separate segments (Figure 15d). Male left fifth legs with four segments, right leg about half as long and trimerous (Figure 18q).

Total length: Adult female: range 3.63 to 4.65 mm, mean = 4.10 mm, $s = 0.2900$, $N = 28$ (Figure 16).

Adult male: range 2.93 to 3.50 mm, mean = 3.135 mm, $s = 0.1775$, $N = 7$. Specimens selected at random from localities listed in Table 1.

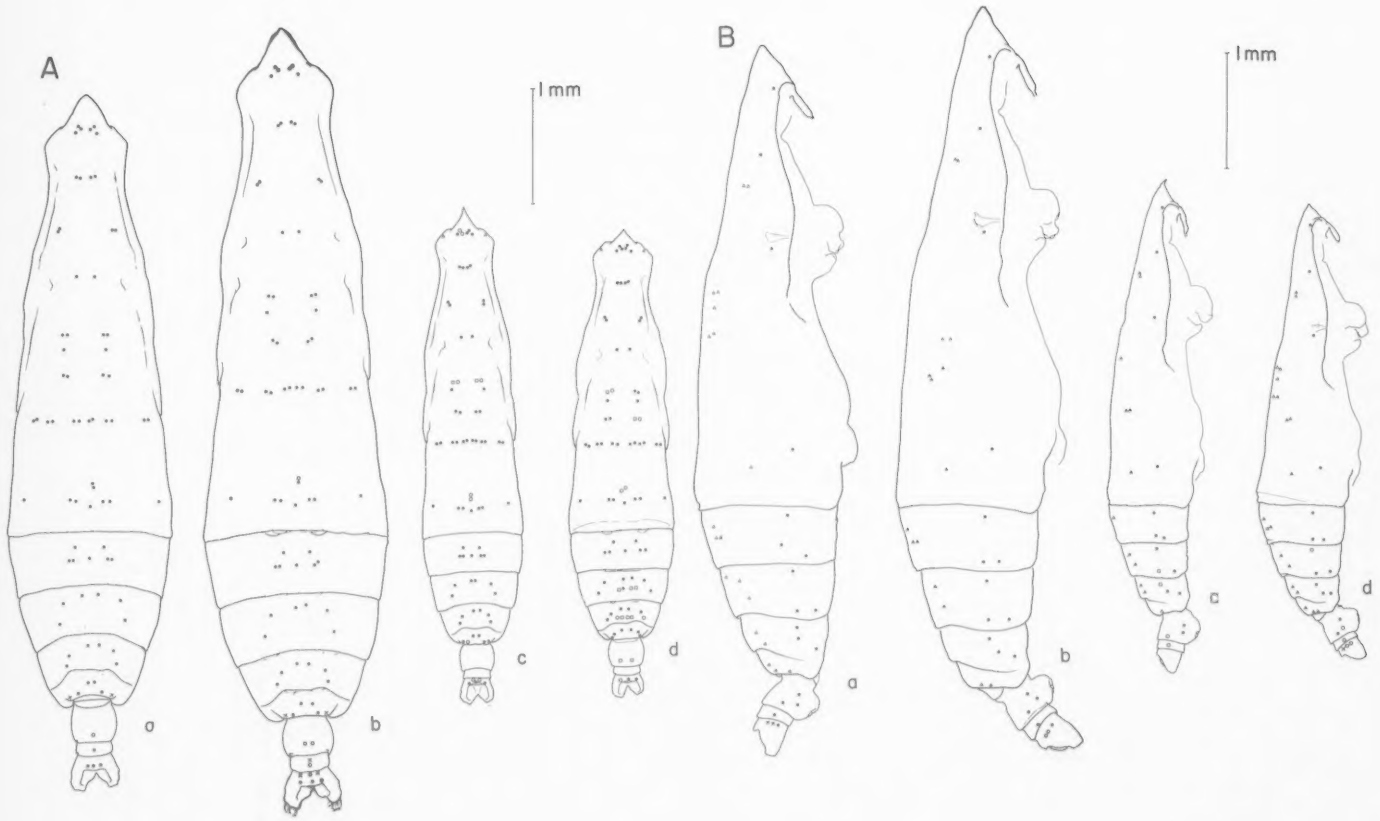


FIGURE 15.—Species of the attenuatus group of *Eucalanus:* **a.** *parki,* **b.** *langae,* **c.** *sewelli,* **d.** *attenuatus*. Dots represent sites occurring at a frequency of 100% in the pooled sample of the species; open circles are sites appearing in 80 to 99% of the pooled sample; crosses are sites occupied in from 10 to 79% of the pooled sample. Open triangles are sites also visible in lateral view but assigned to tergal sets. Dorsal view on left, lateral view on right. All figures of adult females made with the aid of a camera lucida.

Geographical distribution: Verified localities (Figure 17) suggests a broadly tropical distribution restricted to the Indian and Pacific Oceans. A deliberate search among several hundred plankton samples from Atlantic Ocean localities scattered over the lower latitudes failed to yield a single specimen of *attenuatus* s.s. The species is widespread in tropical latitudes of the Indo-Pacific but appears to be most abundant immediately downstream of eutrophic regions along the equator.

Reference: Three lots of reference specimens deposited in the U.S. National Museum (USNM).

2 ♀♀. USNM 143848. Cruise Dodo VI, stn 49, 1-m net, 0-200 m wire out (MWO); 20 Aug. 1964, 1445-1500 h; 10°19′N, 53°11′E.

3 ♀♀. USNM 143849. Cruise Dodo VI, stn 47, 1-m net, 0-200 MWO; 19 Aug. 1964, 1825-1840 h; 8°53′N, 53°09′E.

1 ♀. USNM 143850. Cruise Scot (TO58-1), stn 35, 1-m net, surface; 7 May 1958, 0343 h; 9°45′N, 96°04′W.

Remarks: Dana's (1849, p. 18, 19) first locality given for *attenuatus* is from the vicinity of the Kingsmill (=Gilbert) Islands in the western Pacific (13 April 1841). Other U.S. Exploring Expedition localities include the China Sea at about lat. 5° to 10°N (15 February 1842) and the Sulu Sea (2 February and 2 March 1842). All of these localities lie in Indo-Pacific tropical waters, the biogeographical zone and the geographical region that yielded most of the records of *attenuatus* s.s. Moreover, Dana's figures (1853, Figure 2d, e) of *attenuatus*, while crude emphasize a short wide-angled forehead characteristic of the tropical population.

Vervoort (1946) noted two morphological kinds of *attenuatus* s.l. in *Suellius* collections, and his illustration (Figure 7c) probably refers to *attenautus* s.s.

Sewell's (1947) description of *pseudattenuatus* shows a pattern of integumental organs ascribable to the tropical species *attenuatus* s.s. His illustration of *attenuatus* (1947, Text Figure 7B) appears on the basis of an incomplete account of integumental organs and the forehead to be referrable to *sewelli* described below.

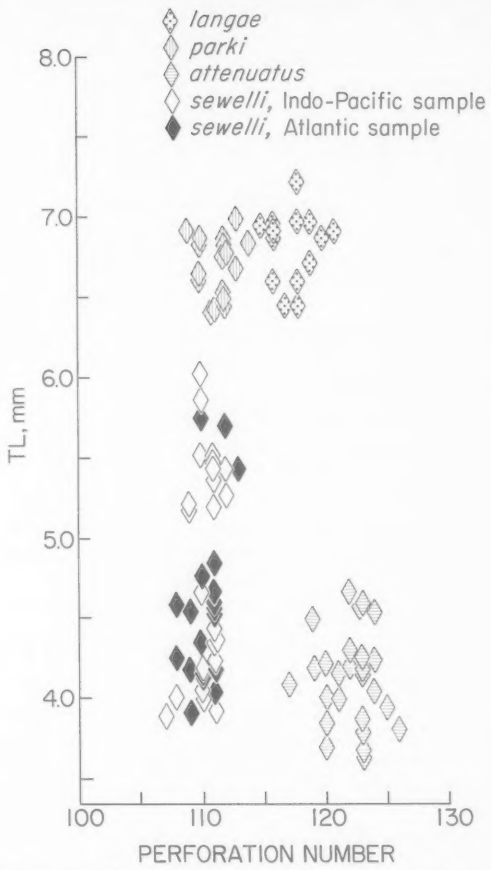


FIGURE 16.—The attenuatus group of *Eucalanus*. Perforation number plotted against total length (TL) in adult females comprising the pooled samples.

Brodsky's (1962) description of *pseudattenuatus* may be based on *attenuatus* s.s., but the figures fail to provide adequate details of the forehead and the absence of information on dorsal integumental organs on ThIII and ThIV leave the issue open.

Eucalanus sewelli, n. sp.
(Figures 1r, 15c, 18b-d, o, r)

E. attenuatus: Vervoort 1946, p. 95-103 (pars), Figs. 7d-f; Sewell, 1947, p. 39, Text-fig. 7B; Brodsky 1962, p. 113, Fig. 14.

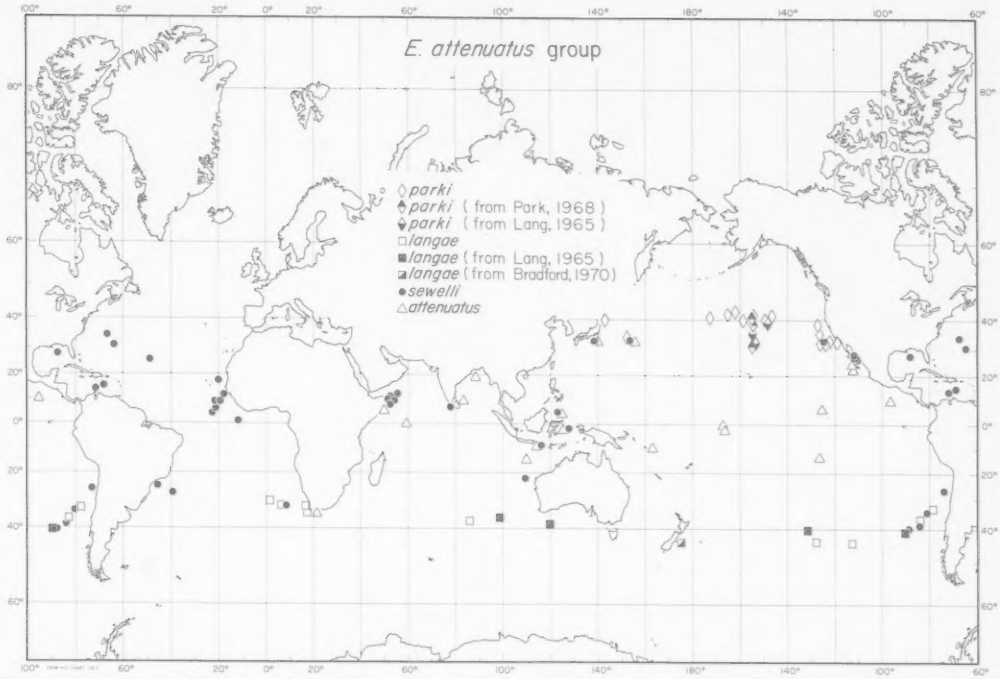

E. attenuatus group
◊ parki
▲ parki (from Park, 1968)
▼ parki (from Lang, 1965)
□ langae
■ langae (from Lang, 1965)
◪ langae (from Bradford, 1970)
● sewelli
△ attenuatus

FIGURE 17.—Geographical localities of the species in the attenuatus group. All identifications except those of Park (1968) and Bradford (1970) verified by examination of integumental organs.

Diagnosis: Adult female with mandibular basis bearing two setae as in *attenuatus*. Differs from *attenuatus* in designated sites on ThIII and ThIV, each of which lacks the two pairs of tergal sites enclosed by the outer arc of six tergal sites (Figure 15c). Genital segment lacking integumental organs. Abd.IV-V with two transverse tergal rows and lacking pleural sites (Figure 15c).

Adult male: Tergal sites on ThIII and ThIV as in female. Abd.II lacking dorsal integumental organs (Figure 18i). Mandibular basis with two setae.

Additional description: Adult female with forehead more strongly attenuated and longer than that in *attenuatus* (Figure 15c), apex usually curving weakly ventrad (Figure 18c). In relatively eutrophic regions of the Indo-Pacific *attenuatus* and *sewelli* may co-occur and resemble one another in size and general morphology, but differences in integumental organs persist. In strongly eutrophic tropical regions *sewelli* may exceed 6 mm in TL and exhibit a more prominent conical forehead with rounded apex (Figure 18d). Male with fifth pair of legs as in *attenuatus* (Figure 18o, r).

Total length: Adult female: range 3.89 to 6.10 mm, mean = 4.720 mm, s = 0.6350, N = 43 (Figure 16).

Adult male: range 2.89 to 4.58 mm, mean = 3.195 mm, s = 0.4680, N = 14. Specimens selected at random from localities listed in Table 1.

Geographical distribution: Verified localities (Figure 17) indicate a circumglobal range in eutrophic tropical and subtropical waters extending to the subtropical convergences.

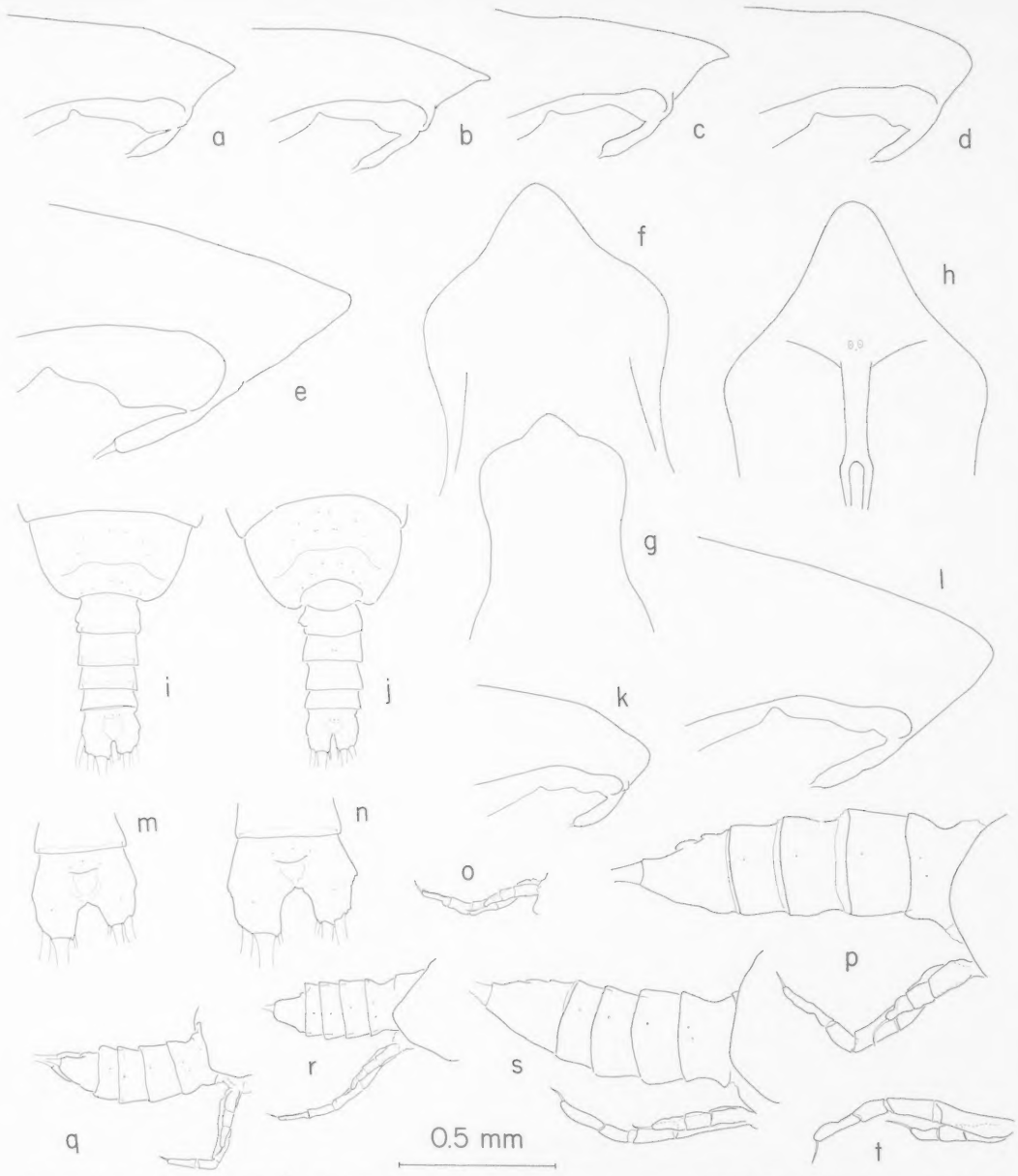


FIGURE 18.—Anterior portion of head, lateral view, female; **a.** *Eucalanus attenuatus* (EQUAPAC S 21); **b.** *sewelli* (*Alaska* 5-9); **c.** *sewelli* (Naga S11A 61-198); **d.** *sewelli* (CalCOFI 5708 144.G15); **e.** *parki* (Boreas 19). Anterior portion of head, dorsal view, male; **f.** *parki* (Zetes 14); **g.** *attenuatus* (EQUAPAC S 21). Anterior of head, ventral view, female; **h.** *langae* (Lusiad 14). ThIV-V and abdomen, dorsal view, male; **i.** *sewelli* (CalCOFI 5708 144.G15); **j.** *attenuatus* (EQUAPAC S 21). Anterior portion of head, lateral view, male; **k.** *attenuatus* (EQUAPAC S 21); **l.** *parki* (Zetes 14). Anal segment and fused furcal rami, dorsal view, male; **m.** *parki* (Zetes 14); **n.** *attenuatus* (Monsoon 24). Fifth pair of legs, male, right lateral view; **o.** *sewelli* (CalCOFI 5708 144.G15); **p.** *langae* (Lusiad VII MWT 19); **q.** *attenuatus* (EQUAPAC S 21); **p.** *sewelli* (*Alaska* 5-9); **s.** *parki* (CalCOFI 5804 80.130); left lateral view; **t.** *parki* (Boreas 19). Positions for stations mentioned are listed in Snyder and Fleminger (1965, 1972).

Types and type locality: Holotype: ♀. USNM 143844. Cruise Downwind, stn 23a, 45-cm net, 0-352 m; 19 Oct. 1957, 0000-0100 h; 38°46′S, 83°20′W.

Reference: 3 ♀♀. USNM 143845. Cruise Downwind, stn 28, 1-m net, 0-283 m; 31 Dec. 1957, 0520-0542 h; 27°08.5′S, 72°02′W.

3 ♀♀. USNM 143846. Cruise Atlantis II-13, stn 8, ¾-m net, depth? 5 Oct. 1964, 1410-1435 h; 41°26′N, 55°45′W.

1 ♀. USNM 143847. Cruise Dodo VI, stn 55, 1-m net, 0-200 MWO; 22 Aug. 1964, 1845-1858 h; 10°14′N, 51°19′E.

Remarks: Brodsky's (1962, p. 113) record of (?) *attenuatus* appears from his illustration (Figure 14) and the locality off northern Japan to be referable to *sewelli*. Other records that appear to be assignable to *sewelli* include Tanaka (1956, p. 266, Figure 4a), Ramírez (1969), and Roe (1972). This species is named to honor R. B. Seymour Sewell who among his many significant contributions to the copepod literature inspired study of their integumental organs and directed attention to the complexity existing in the attenuatus group.

Eucalanus parki, n. sp.
(Figures 1s, 15a, 18e, f, l, m s, t)

E. attenuatus: Park 1968, p. 533, Pl. 1, Figs. 16, 17, Pl. 2, Figs. 1-16, Pl. 3, Figs. 1-13, large form only.

Diagnosis: Adult female: Mandibular basis with four setae. Sites of integumental organs similar to those of *sewelli* except for presence of one medial tergal site on both the genital segment and on Abd.III, one or more pleural sites on Abd.IV-V, and only one transverse tergal row on Abd.IV-V (Figure 15a).

Adult male: Forehead prominent, protruding as an elongate triangle about twice as far beyond base of rostrum as in *sewelli* and *attenuatus* (Figure 18f). Integumental organs on cephalosome and thorax as in female; Abd.II with or without one tergal site (in 11 specimens, 6 with and 5 without). Mandibular basis usually with four setae, one specimen in 11 with three setae.

Additional description: Adult female with conical forehead and rounded apex as in Figure 18e, differs from typical acutely pointed forehead of *sewelli*.

Total length: Adult female: range 6.40 to 7.17 mm, mean = 6.744 mm, s = 0.1982, N = 18 (Figure 16).

Adult male: range 5.20 to 5.96 mm, mean = 5.620 mm, s = 0.2380, N = 10. Localities of specimens listed in Table 1, pooled sample represents all adults on hand.

Geographical distribution: All records (Figure 17) are from the North Pacific Ocean. Most fall within the Transition zone (Brinton, 1962, p. 202) but a number also appear along long. 155°W extending south to lat. 32°N, following the line of division between western and eastern North Pacific Central Water (Sverdrup, Fleming, and Johnson, 1942, Figure 209A) which is supported by the relative elevation of the isotherms in the upper 200 m of the mid-latitudes in the North Pacific relative to those of the South Pacific (Reid, 1965, Figure 2).

Types and type locality: Holotype: ♀. USNM 143841. Cruise Norpac H5508, stn 24-42, 1-m net, 0-200 MWO; 21 Aug. 1955; 1556-1610 PST; 40°26′N, 146°37′W.

Reference: 1 ♀, specimen no. 2. USNM 143842. Cruise Norpac H5508, stn 24 (up), 1-m net, 0-200 MWO; 25 Aug. 1955, 1620 PST; 42°17′N, 146°16′W.

1 ♀, specimen no. 1. USNM 143843. Cruise Norpac H5508, stn 25 (up), 1-m net, 0-200 MWO; 25 Aug. 1955, 1816-1831 PST; 42°17′N, 150°00′W.

Remarks: Large forms of *attenuatus* s.l. have been noted from the North Pacific by several authors (e.g., Tanaka, 1956, p. 266, Figure 4b; Lang, 1965 Park, 1968). Park (1968) fully appreciating its distinctiveness described it in detail. He relinquished his original intention of naming it as a distinct species upon my recommendation, which was based on the apparently extensive variability generally thought to prevail in *Eucalanus*. At that time there was no reliable basis for distinguishing genetic from phenetic variation and reliable capture records

were insufficient to provide an indication of biogeographical affinities. It is a great pleasure to name this species for TaiSoo Park in recognition of his acumen and farsightedness in judging copepod systematics.

Eucalanus langae, n. sp.

(Figures 1t, 15b, 18h, p)

E. attenuatus: Bradford 1970, p. 353, Figs. 6-9.

Diagnosis: Adult female: Closely resembling *parki* in size and appearance including the occurrence of four setae on the mandibular basis. Integumental organs as in *parki* except for significant increase in abdomen (Figure 15b). Genital segment and Abd.III each with two tergal sites. Anal segment (Abd.IV-V) with two transverse rows of tergal sites as well as more regularly occupied pleural sites occurring in copepodid stage V and in adults (Figure 19, Table 5), the mean total number being about twice that of *parki*.

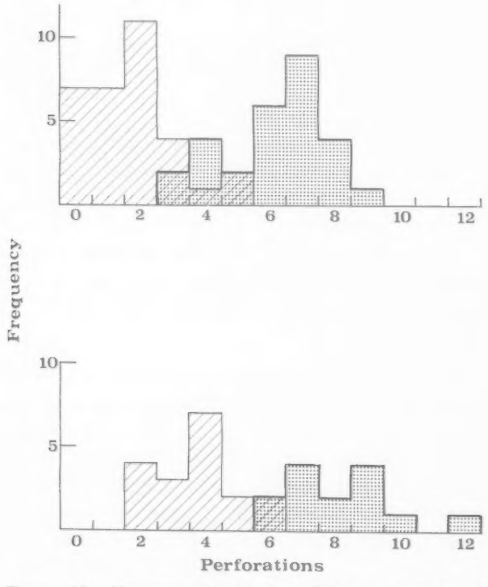


FIGURE 19.—Frequency distribution of the total number of perforations on the anal segment (Abd.IV-V) in stage V female copepodids above and in adult females below. Diagonal hashing represents *Eucalanus parki*, dotted area represents *E. langae*.

Additional description: Adult male: Integumental organs of cephalosome and thorax as in female; Abd.II with two tergal sites as in genital segment of female.

Total length: Adult female: range 6.44 to 7.22 mm, mean = 6.847 mm, $s = 0.2235$, $N = 14$ (Figure 16).

Adult male: 6.12 mm and 6.59 mm. Localities of specimens given in Table 1.

Geographical distribution: Available records (Figure 17) indicate that *langae* is a resident of the circumglobal Transition zone in the Southern Hemisphere.

Types and type locality: Holotype: ♀. USNM 143839. Cruise Lusiad VII, stn 14, Isaacs-Kidd midwater trawl; 0-3,400 m; 6 June 1963, 1530-2300 h; 32°30′S, 9°04′E to 32°24′S, 8°25′E.

Reference: 2 ♀♀, specimens no. 4 and 6. USNM 143840. Cruise Monsoon, stn 18, Isaacs-Kidd midwater trawl; 0-2,723 m; 11 Mar. 1961, 2046-0303 h; 25°52′S, 155°44′W to 25°40′S, 155°34′W.

Remarks: Lang (1965) found specimens of this species at several Monsoon and Downwind stations (Figure 17) and noted their resemblance to their North Pacific temperate cognate. Bradford (1970) also noted this similarity in recording it from off the Kaikoura Peninsula, New Zealand, and referring to Tanaka's (1956) mention of a large *attenuatus* s.l. off Japan.

Though data on designated sites are lacking for Bradford's specimens, the probability that they are referable to *langae* is sufficiently great to include them under the species without reservation.

Assignment of the sibling populations *langae* and *parki* to separate species is based on two lines of evidence: 1) significant differences in designated sites involving abdominal segments that undergo modification with sexual maturation (Table 5, Figure 19); 2) apparent restriction of each population to temperate zones in opposite hemispheres (Figure 17).

Although data on actual depth distribution are unavailable for either species, most of the

TABLE 5.—Number of perforations on anal segment of *parki* and *langae* in copepodid stage V and adult females of *Eucalanus*.

Species	Range	$\bar{x}$	s	N	t	P
parki: stage ♀	0-5	1.75	1.4368	32		
adult ♀	2-6	3.7222	1.2744	18		
langae: stage V ♀	3-9	6.1428	1.6036	28		
adult ♀	6-12	8.1428	1.6576	14		
Comparison of sample means of female specimens						
parki stage V and adult ♀				50	4.85	<0.001
langae stage V and adult ♀				42	3.76	<0.001
stage V: *parki* and *langae*				60	11.193	<0.001
adults: *parki* and *langae*				32	8.55	<0.001

records of *langae* and *parki* (Table 1) are based on relatively shallow tows with open nets from 300 m or less to the surface. Following the shortest prevailing surface circulation in the Pacific Ocean, shallow water passage from the temperate zone of one hemisphere to that of the other is at least 9,000 miles long. It would begin necessarily in the eastern boundary currents and continue in the equatorial circulation where crossover to the succeeding western boundary current in the opposite hemisphere might occur. Assuming a high rate of 1 knot and an unrealistic expectation of continuous and direct transport would require a transit time exceeding 1 yr.

Among my unpublished records of *attenuatus* s.l. neither *langae*- nor *parki*-like individuals of any copepodid stage appear in the equatorial localities (cf. Fleminger and Hulsemann, 1973, for geographical distribution of samples that have been examined for *Eucalanus*). Moreover, no specimens that might be attributable to *langae* or *parki* on the basis of unusually large size appear among the published records of *attenuatus* s.l. collected from the vicinity of the Pacific's equatorial circulation.

Transhemispheric passage at subsurface depths would be at transport rates that are probably an order of magnitude less than surface transport. Evidence of tropical submergence by *attenuatus* s.l. is lacking, however, despite widespread studies on the vertical distribution of copepods in the upper 500 m of the Pacific. Also, *attenuatus* s.l. appears to be a fine particle filter-feeder (Mullin, 1966; Samyshev, 1970) and therefore not a likely candidate to survive deep submergence to meso- or bathypelagic depths for periods of one or more years. In the light of this background the relatively small but constant morphological differences and an apparent allopatry, maintained by the formidable barrier of the tropical and subtropical zones separating the ranges of *parki* and *langae*, provide compelling reasons for treating the two biantitropical (Brinton, 1962) populations as separate species.

If *langae* could survive transport to temperate waters of the Northern Hemisphere it could be expected to appear in the North Atlantic Drift. Despite the great intensity of study on oceanic copepods of the North Atlantic no "giant" *attenuatus* s.l. forms have been noted from the region. With (1915, p. 52-53, Pl. 1, Figure 6a-c, Text figure 10a-e) reports several large *attenuatus* s.1. stage V copepodids (♀ = 5.18 mm, ♂ = 5.0 mm) collected at two North Atlantic localities lying roughly between Iceland and Scotland. With notes that "The structure of the mouth appendages . . . scarcely show differences of any importance from Giesbrecht's description . . .". Thus it seems likely that the mandibular basis in his specimens bore two setae as in *sewelli*, a species that reaches a length in accord with With's measurements (Figure 16 and see p. 993 above). The absence of other reports of large *attenuatus* s.l. in excess of 6 mm in TL from the North Atlantic even at considerable depths (e.g., Roe, 1972) further substantiates the lack of a North Atlantic temperate cognate of *parki* and *langae*.

The species is named for Bui Thi Lang to acknowledge her discovery (1965) of morphological and geographical complexity in *attenuatus* s.l.

KEY TO THE SPECIES OF *EUCALANUS*

(Adult Females Only)

Based on integumental organs, all sites are tergal unless specified otherwise.

1. Mxp with four or more pairs of sites; ThIII and IV lacking single middorsal site between anterolateral hair sensilla; ThIV lacking paired sites lying outside of dorsal quadrangle of hair sensilla 2

   Mxp usually with two pairs of sites; ThIII and IV with single middorsal site lying between anterior two hair sensilla; ThIV with one pair of sites lateral to quadrangle formed by four hair sensilla 3

2. Mx1 and Mx2 with total of 10 sites forming a rectangle and arranged anterior to posterior in two bilateral sets of one pair, one single and one pair of sites; ThII and III in lateral view with three sites, Abd.IV-V with at least three tergal sites .....attenuatus group, 4

   Mx1 and Mx2 sites vary from 8 to 18 in number, not arranged in rectangle pattern, posterior sets more lateral than anterior sets; ThII and III with one or two lateral sites; Abd.I-II with at least two tergal perforations .....elongatus group, 5

3. ThIII and IV with one medial site in tergal arc formed by the tergal sites .....subtenuis group, 6

   ThIII and IV with two medial sites in the arc formed by the tergal sites .....pileatus group, 7

4. A. Abd.III with tergal site ..... B

   Abd.III lacking tergal site C

   B. Abd.I-II usually with one site, Abd.IV-V with three tergal and one pleural site ..... *parki*

   Abd.I-II usually with two sites, Abd.IV-V with at least four tergal and three pleural sites ..... *langae*

   C. Abd.I-II lacking tergal sites, Abd.IV-V usually with five tergal and zero pleural sites ..... *sewelli*

   Abd.I-II with two tergal sites, Abd.IV-V with three tergal, usually two or more pleural sites ..... *attenuatus*

5. A. ThII and III with a pair of sites anterolateral to arc formed by tergal sites; Mx1 and Mx2 with at least 16 sites ..... B

   ThII and III lacking a pair of sites anterolateral to arc formed by tergal sites, Mx1 and Mx2 with 12 or fewer sites ..... D

   B. ThI and II each with seven tergal sites; Abd.I-II with three tergal sites ..... *hyalinus*

   ThI with 13, ThII with nine tergal sites; Abd.I-II with four tergal sites C

   C. Mandibular basis with one seta ..... *californicus*

   Mandibular basis with three setae ..... *bungii*

   D. A1 somite with sets of eight and four sites; Mnd somite with six sites; ThV with three sites; Abd.I-II with two sites, Abd.III and IV lacking tergal sites, Abd.IV lacking pleural sites .. *inermis*

   A1 somite with sets of six and two sites; Mnd somite with two to four sites; ThV

with four or more sites; Abd.I-II with four or more sites; Abd.III and IV with two or more sites; Abd.IV with one pleural site ..... *elongatus*

6. A. Mx2 somite with two or more pairs of sites; ThI with seven or more sites; ThII and III with one asymmetrical site within arc of hair sensilla on left of midline; Abd.I-II with two sites ..... B

Mx2 somite lacking sites; ThI with three sites; ThII and III lacking sites within dorsal arc of hair sensilla; Avd.I-II with up to one site C

B. ThI with 15 sites; Mx1 somite with 10 sites including a medial set of four; A1 somite with 10 sites including a posterior set of four; Mnd somite with eight sites . *subtenuis*

ThI with seven sites; Mx1 somite lacking four medial sites; A1 somite lacking four posterior sites; Mnd somite with four to six sites ..... *mucronatus*

C. ThII and III with three pleural sites, Abd.IV-V with three tergal sites ..... *monachus*

ThII and III with two pleural sites, Abd.IV-V with one tergal site ..... D

D. Mnd somite with six sites; Abd.I-II lacking tergal sites .. *crassus*

Mnd somite with four sites; Abd.I-II with one tergal site ..... *longiceps*

7. A. ThII and III with two pairs of pleural sites; Mx2 somite with two pairs of tergal sites; Abd.I-II with three sites; Abd.III with two sites ..... B

ThII and III with one pair of pleural sites; Mx2 somite lacking tergal sites; Abd.I-II usually with one site; Abd.III lacking tergal sites ..... *pileatus*

B. Mx1 somite with two pairs of sites adjacent to the midline; Abd.IV-V with one site ..... *subcrassus*

Mx1 somite with one pair of sites adjacent to the midline; Abd.IV-V with three sites ..... *dentatus*

USE OF INTEGUMENTAL ORGANS IN STUDIES ON GEOGRAPHICAL VARIATION

A relatively high degree of variability in perforation number was noted for the circumglobal, broadly tropical species, *E. subtenuis* (Table 4, Figures 9, 10). The conspicuous variability was noticed after realization that bilateral symmetry and arrangement in regular patterns distinguishing species groups as well as species is characteristic of integumental organs. The variation suggested that these organs are a promising source to search for evidence of genetic variation in field-collected planktonic populations. Thus to carry out a pilot study of this possibility the original sampling of *subtenuis* was supplemented by additional specimens sorted at random from zooplankton samples selected to represent both extreme and intermediate geographical locations within the known distribution in each ocean (Figure 20). For each specimen pleural perforations were tallied from both left and right sides of the entire body and summed with counts of the tergal perforations to obtain a maximum estimate referred to as the perforation number (PN). TL was also measured routinely using procedures described in the section on Material and Methods. It should be noted that no attempt was made to determine the existence of geographical variation in any

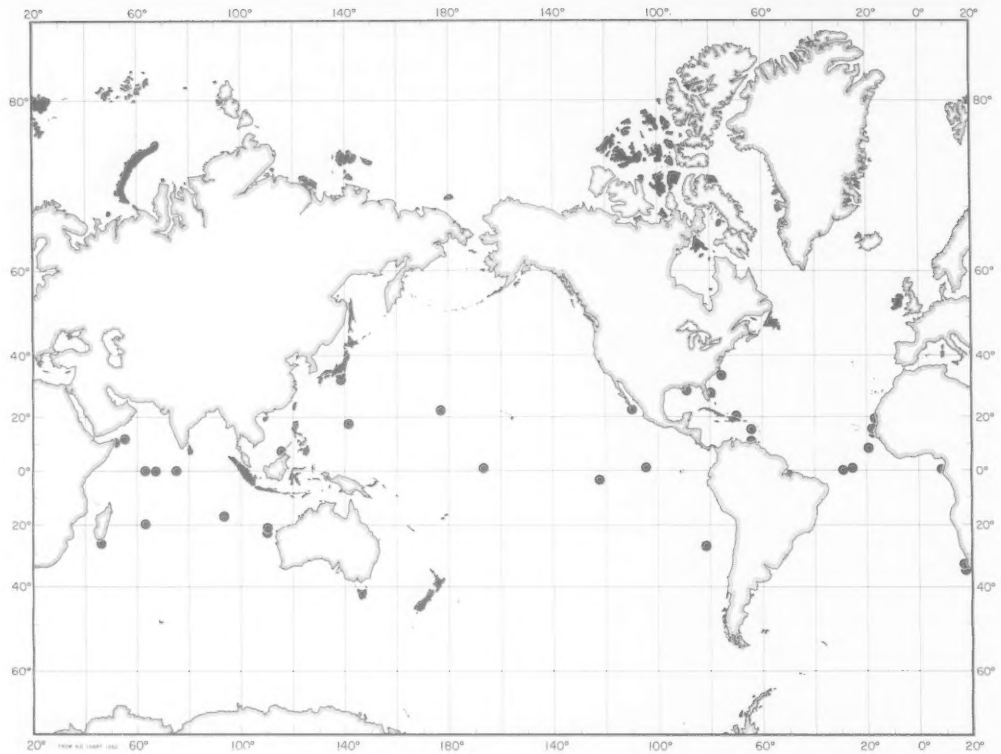


FIGURE 20.—Geographical distribution of *Eucalanus subtenuis*. Localities shown based on records verified by analysis of integumental organs.

other morphological features of *subtenuis* except to confirm that in virtually all specimens from each ocean the mandibular basis bore three setae as found by Fukase (1957).

The data were first examined by pooling the samples from each ocean and comparing the mean number of perforations between oceans. Differences between the pooled samples proved to be highly significant (Table 6), and the mean PN values show a pronounced geographical trend. The lowest mean was obtained from the Pacific Ocean specimens and the highest from the Atlantic Ocean specimens. The pooled sample from the Indian Ocean yielded a mean PN virtually midway between the other two.

The gross indication of clinal variation suggested further consideration at a finer scale.

The PN counts of *subtenuis* were regrouped by geographical source of the specimens in units of 60° of longitude and compared in terms of frequency distribution and mean PN per geographical segment (Figure 21). Grouped samples falling within the hydrographic limits of any one ocean do not differ significantly (Table 7) and serve to emphasize the stepped or discontinuous pattern of the means from the different oceans. The range shown by PN in the two geographical segments between long. 30°E and 150°E (Indian Ocean and westernmost Pacific Ocean) spans the apparent differences in the distribution of PN in the Pacific and Atlantic samples (Figure 21). Thus the Indian Ocean population would appear to be the one genetically and geographically intermediate in

TABLE 6.—Total number (PN) of perforations in samples of *Eucalanus subtenuis* from different oceans.

Sample	Range	$\bar{x}$	s	s^2	N	t	P
Pacific Ocean	114-135	123.6388	4.9750	24.7506	36		
Indian Ocean	119-139	130.0416	4.9911	24.9111	24		
Atlantic Ocean	125-141	134.8400	3.2598	10.6263	50		
Comparison of differences between mean number (Student's t - test)							
Pacific : Indian					60	4.877	<0.001
Indian : Atlantic					74	4.98	<0.001
Atlantic : Indian-Pacific combined					110	9.37	<0.001

position to those of the Pacific and Atlantic populations, a pattern consistent with the prevailing surface circulations of equatorial and western boundary currents.

When the various sets of perforations are analyzed separately, however, the resemblance of the variation to either a zone of intergradation or a stepped cline disappears. The designated sites in *E. subtenuis* fall into 26 tergal and 13 pleural sets based on the scheme described above (Figures 5, 7). More than half of these sets show zero or negligible variability, i.e., typical perforations were observed at these sites in virtually all of the specimens. Most of the variation was in fact concentrated in only nine sets of designated sites (Figure 22a, b).

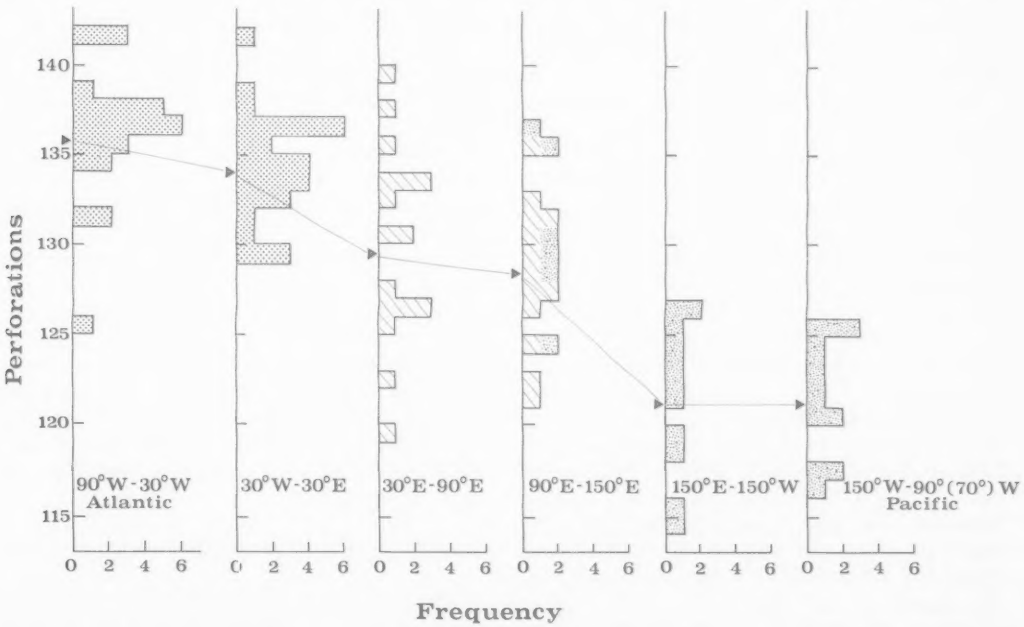


FIGURE 21.—Frequency distribution of total number (PN) of perforations per specimen in samples of adult females of *Eucalanus subtenuis* collected within 60° segments of longitude. Uniform large spot shading represents specimens collected at localities in the Atlantic Ocean; obliquely ruled shading represents specimens collected at localities in the Indian Ocean; irregular finely dotted shading represents specimens collected at localities in the Pacific Ocean. Differences between the means in the second and third histograms and the fourth and fifth histograms counting from the left are highly signifiicant (t-test, Table 7). Black triangle indicates position of mean PN within geographical segment. All specimens selected at random from zooplankton samples located in various sectors of the *subtenuis* range (Figure 20).

TABLE 7.—Comparison by Student's *t*-test of mean TN values of samples of adult female *subtenuis* grouped regionally as in Figure 21 in segments of 60° of longitude.

Regional segments (longitude)	N_1+N_2	$\bar{x}$	t	P
90°-30°W : 30°W-30°E	52	135.74 : 134.00	1.99	$<0.1\ P>0.05$
30°W-30°E : 30°-90°E	45	134.00 : 129.56	3.59	<0.001
30°-90°E : 90°-150°E	35	129.56 : 128.68	0.54	$<0.6\ P>0.5$
90°-150°E : 150°E-150°W	30	128.68 : 121.18	5.623	<0.001
150°E-150°W : 150°-90°(70°)W	23	121.18 : 121.25	0.064	>0.9
150°-90°(70°)W : 90°-30°W	35	121.25 : 135.74	11.91	<0.001

The nine sets appear to vary independently of one another, some showing unusually high or low frequencies of absence in one or two of the three oceans. In some sets the frequency of absence in one ocean differs significantly from that elsewhere (Figure 22a, b; Table 8). Within each set perforations tend to be absent at similar frequencies. Genetic linkage is suggested by the similar deviations in the Pacific sample affecting the following sets: Mx1-T-a-*l*3, 4, r3, 4; Mxp-T-*l*1, 2, r1, 2; ThII-P-*l*a1, ra1; ThIII-P-*l*a1, ra1; and ThIV-P-*l*a1, ra1.

Also unique to the Pacific sample is the more frequent occurrence of four perforations on the somite of the first maxilla (Mxl-T-d-*l*1, 2, r1, 2). The Indian Ocean sample is distinguished by a relatively infrequent appearance of the set of perforations on the somite of the second antenna (A2-T-a-*l*1, 2, r1, 2). The Atlantic sample shows relatively few absences on the Mx1 somite (Mx1-T-c-*l*1, 2, r1, 2) and on ThII (ThII-T-a-*l*2, 3, r2, 3).

In an individual specimen perforations are often absent in pairs rather than in full sets though right and left pairs in a set tend to show similar frequencies in the sample. Absences of peg and pore combinations are usually bilateral and affect both the right and left sides of a particular set. Absences of pairs consisting of a pit sensillum and a pore may be bilateral but more frequently affect only one side in a specimen. An appreciable portion of the variability in *subtenuis* emanates from losses among such tergal pairs occurring sequentially on the two maxillary somites. An individual specimen may show losses that alternate in successive sets from either left to right or the reverse. A noticeable trend in losses toward unbalanced symmetry was found only in the case of Mx1-T-b-*l*1, 2, r1, 2. Indian and Atlantic samples showed more absences on the right side and Pacific samples had a higher frequency of absence on the left side, but the differences are significant (χ^2 test for homogeneity) only in the case of the Indian Ocean sample (Table 9). Critical examination for patterned variation among specimens using larger samples may prove to be especially useful for genetic studies on natural and laboratory populations of planktonic copepods.

Despite the relatively frequent absences, each of the 110 specimens of *subtenuis* comprising the combined global sample exhibited a representative perforation pattern permitting identification to species by this feature alone. Also noteworthy is the qualitative resemblance in characters distinguishing the geographical populations of *subtenuis* and differences separating *parki* from *langae*. As in *subtenuis* few perforations distinguish these allopatric temperate species of the attenuatus group from one another, and the sites involved are also restricted to a limited portion of the body (i.e., the abdomen and especially Abd.IV-V). The parallels emphasize the likelihood of appreciable genetic discontinuity separating Atlantic, Indian, and Pacific populations of *subtenuis* that deserves more intensive study.

SIZE AND PERFORATION NUMBER

The perforation number (PN), i.e., the number of designated sites in the species observed on each specimen is derived from a meristic complex of integumental organs. The two organ systems, sensilla and glandular pores, are arranged in serially homologous sets that are distributed on all body segments. Showing phylogenetic and species specific patterns, they

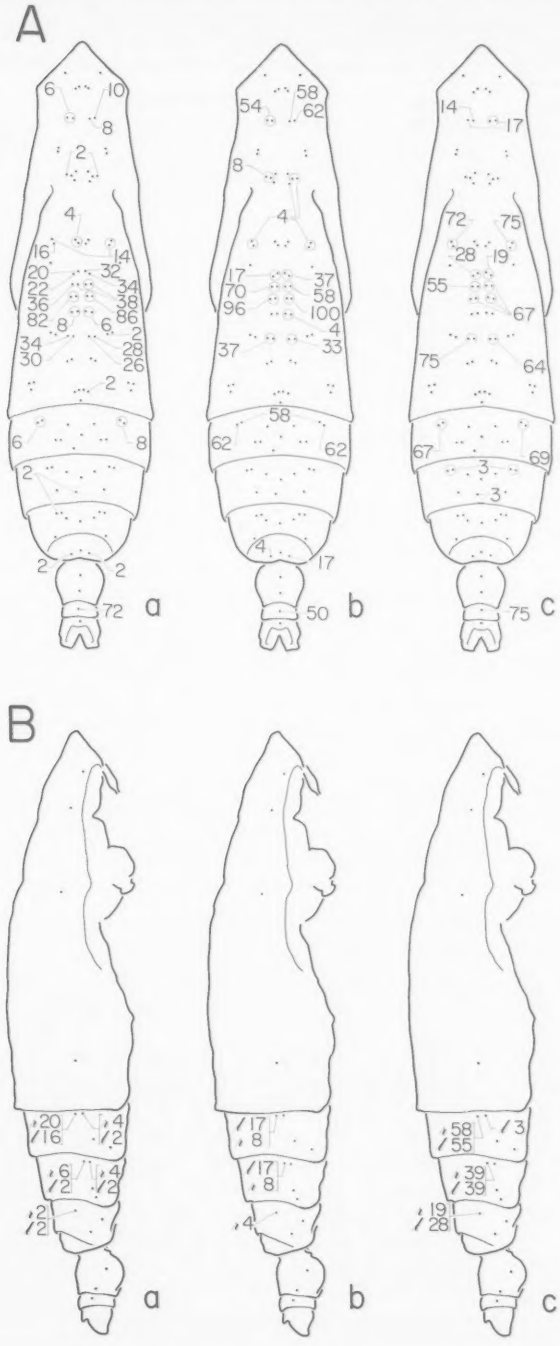


FIGURE 22.—Variation in the occurrence of perforations at designated sites in three regionally pooled samples of *Eucalanus subtenuis* adult females. Sampling localities shown in Figure 20 and geographical grouping based on significant differences between geographical regions shown in Table 7. From the left: Atlantic Ocean sample (N = 50), Indian Ocean sample (N = 24), Pacific Ocean sample (N = 36). Dots represent perforation sites typical of the species. Numbers represent percentage of specimens lacking a perforation at this site; open circles enclose pairs of sites showing the same frequency of absence. Absence of a number indicates perforation found in all specimens of the sample. Dorsal view top; right lateral view bottom.

TABLE 8.—χ^2 test for homogeneity of frequency of absence of perforations from designated sites among geographically different samples of *Eucalanus subtenuis* adult females described in Figures 20 and 21.

Regional sample	Frequency of absences			Atl., Ind., Pac. compared		Atl., Ind. compared		Atl., Pac. compared		Ind., Pac. compared		Largest source of χ^2
N	Atl. 50	Ind. 24	Pac. 36	χ^2	*P*2d.f.	χ^2	*P*1d.f.	χ^2	*P*1d.f.	χ^2	*P*1d.f.	
Designated sites (no.)												
A2-Ta $\Sigma l1,2;r1,2$ (4 sites)	15	55	23	99.8	<0.001	89.2	<0.001	5.28	<0.025 *P*>0.01	44.6	<0.001	Indian
Mx1-Ta $\Sigma l3,4;r3,4$ (4 sites)	29	4	106	179.9	<0.001	6.98	<0.01 *P*>0.005	122.2	<0.001	108.2	<0.001	Pacific
Mx1-Tc $\Sigma l1,2;r1,2$ (4 sites)	75	62	88	27.5	<0.001	19.1	<0.001	18.7	<0.001	0.26	<0.75 *P*>0.5	Atlantic
Mx1-Td $\Sigma l1,2;r1,2$ (4 sites)	168	94	96	39.3	<0.001	12.3	<0.001	14.1	<0.001	29.1	<0.001	Atlantic
Mxp-T $\Sigma l1,2;r1,2$ (4 sites)	59	34	100	57.7	<0.001	1.0	<0.5 *P*>0.25	53.8	<0.001	27.1	<0.001	Pacific
ThII-Ta $\Sigma l2,3;r2,3$ (4 sites)	14	58	98	156.2	<0.001	100.7	<0.001	142	<0.001	1.48	<0.25 *P*>0.1	Atlantic
ThII-Pr,*l* $\Sigma a1$ (2 sites)	4	6	28	32.3	<0.001	~0.8	<0.5 *P*>0.25	22.2	<0.001	18.0	<0.001	Pacific
ThIII-Pr,*l* $\Sigma a1$ (2 sites)	4	6	28	33.3	<0.001	3.7	<0.1 *P*>0.05	30.2	<0.001	8.3	<0.005 *P*>0.001	Pacific
ThIV-Pr,*l* $\Sigma a1$ (2 sites)	2	1	17	26.0	<0.001	0	>0.9	18.7	<0.001	9.5	<0.005 *P*>0.001	Pacific
No. χ^2 with $P \leq 0.5$					9		5		9		7	

are the unmistakable phenetic expression of the genotype.

Body size (TL) is a priori also under genetic control, and probably in copepods this control is rigorous (Brooks and Dodson, 1965; Brooks, 1968; Dodson, 1970; June and Carlson, 1971). However, it is known that in addition to selection pressures diet and temperature may strongly influence size determination (Coker, 1933; Deevey, 1960, 1964, 1966; Omori, 1970). A question of immediate concern is whether TL and PN may be sufficiently related to show similar phenetic patterns of variation.

Morphogenesis during the copepodite phase of ontogeny appears to affect PN in a simple predictable fashion. In general, copepodid stages III, IV, and V were found with the same number and arrangement of sites, segment by segment, as they appear in adults of the species with exceptions in abdominal segments as indicated above. The exceptions noted are restricted to ontogenetic modifications in the addition of abdominal segments and subsequent fusion of segments brought on by sexual maturation. Thus at least during the second half of ontogenesis integumental organs maintain numerical and distributional relationships during typical size increases associated with moulting; no observations are available for copepodite stages I and II. If a relationship exists between TL and PN it should be apparent from comparison of the two within a given onto-

TABLE 9.—Frequency of absence of perforations at a designated site in *Eucalanus subtenuis* (%).

Sample	Designated site: Mx1-T-6 left 1, 2	right 1, 2	X^2, 1d.f.	P
Pacific Ocean	28, 28	19, 19	~1.6	<0.25 $P>0.2$
Indian Ocean	17, 17	37, 37	5.28	<0.025 $P>0.02$
Atlantic Ocean	20, 20	32, 32	3.64	<0.1 $P>0.05$

genetic stage. In making such comparisons, however, it should be recalled that considerations limited to the numerical value of PN is meaningful primarily within a species group. Between groups numerical differences in designated sites may not occur, but the species always differ in topographic arrangement of sets of perforations common to their respective group (Figures 9, 11, 13, 15).

Scatter diagrams of TL and PN (Figures 10, 12, 14, 16) show no common pattern of relationship among the 19 distinguishable populations (i.e., including the three geographical populations of *subtenuis*). Pearson's product-moment correlation coefficients were calculated for the available measurements of each population (Table 10). Eleven were positive correlations and eight were negative, a division indicative of the absence of a real relationship between TL and PN in the genus. Only four of the correlations depart significantly from zero (5% level): three are positive correlations and one is negative. All aspects considered, the four significant correlations, i.e., *subtenuis*, Pacific Ocean (+), *mucronatus* (+), *sewelli* (+), and *monachus* (−) are probably spurious. Thus, as a working hypothesis PN and TL may be considered to vary independently in adult female *Eucalanus*.

These data shed light on another vital question involving TL and PN, namely, whether in fact the two characters are related genetically. We may anticipate that such a relationship would be apparent by the correlation of the two characters in each species group.

Figures 10, 12, 14, and 16 in fact clearly show the absence of uniformity in the relationship of TL and PN across the genus. We find that each group presents a different pattern of relationship between TL and PN.

TABLE 10.—Correlation coefficient (r) of TL and PN in adult females of *Eucalanus*. Original measurements shown graphically in Figures 10, 12, 14, 16.

Species	N	r	P
subtenuis:			
Atlantic	50	0.0241	>0.1
Indian	24	.1683	>0.1
Pacific	36	.3586	<0.05 $P>0.02$
mucronatus	20	.4743	<0.05 $P>0.02$
crassus	10	−.3477	>0.1
longiceps	12	−.3311	>0.1
monachus	17	−.5967	<0.02 $P>0.01$
pileatus	20	−.3556	>0.1
subcrassus	34	.1569	>0.1
dentatus	21	−.0543	>0.1
elongatus	19	−.0518	>0.1
hyalinus	25	.0831	>0.1
inermis	16	.2365	>0.1
bungii	15	−.0434	>0.1
californicus	22	.3241	>0.1
attenuatus	26	−.0498	>0.1
sewelli	43	.3446	<0.05 $P>0.02$
parki	17	.0407	>0.1
langae	14	.0565	>0.1

It would be of considerable interest to know if PN relates to geographical overlap in the breeding range of species of the same species group. Another related question of ecological significance is whether TL varies with the extent to which the range of a species falls outside of the ecological or biogeographic regions typically occupied by the species group.

REMARKS ON THE FUNCTION OF INTEGUMENTAL ORGANS IN *EUCALANUS*

With so few available retinal cells (Vaissière, 1961; Fahrenbach, 1962, 1964; Park, 1966), copepods must locate appropriate sexual partners, couple, and accomplish spermatophore transfer and attachment in the apparent absence of visual contact with the environment. In nature the available methods appear to be eminently successful in preventing hybrid pairing and in ensuring functional placement of the spermatophore's discharge canal on the female genital pore (Fleminger, 1967; Frost and Fleminger, 1968). External chemical and mechanical receptor-effector systems among the Crustacea appear sufficiently diverse to provide adequate non-visual channels mediating the exchange of information required by a relatively complex and efficient, instinctive mating behavior. As in

terrestrial arthropods microanatomical studies on copepods (Lowe, 1935; Fahrenbach, 1962; Park, 1966) reveal a highly organized central nervous system, one that supports innervated integumental sensilla and glands distributed symmetrically over the body. The receptors may monitor the environment, and the effectors may release information in response to appropriate stimulators.

Among semispecies, i.e., somewhat differentiated populations of a superspecies (Mayr, 1970), the primary reproductive barrier is extrinsic inasmuch as potential hybridizers lack access to one another. Assuming no significant contact since the inception of allopatry, intrinsic reproductive barriers, i.e., prezygotic mechanisms, if any, are untested and probably imperfect or nonexistent. Similar populations of recent common ancestry newly brought together through the expansion of ranges are likely to interact unfavorably across a spectrum of fundamental organismic processes and thereby experience pronounced selection pressures. When sympatry replaces allopatry among sets of semispecies hybridization is often intense in the area of geographical overlap (Remington, 1968; Rising, 1970).

The only stabilizing alternatives for such interacting populations are: 1) elimination of one or both; 2) genetic displacement; or 3) coalescence. Alternatives 1 and 2 will prevail if, in general, hybrid offspring are less fit and at a selective disadvantage and only postzygotic barriers are available. Development of increased efficiency of prezygotic barriers will be at a premium and the rate of their development and distribution will be a function of the rate of interactions and the mobility of the populations. According to MacArthur and Wilson (1967) a computer model by Bossert has indicated that full displacement is achieved rapidly and, under ideal conditions, equilibrium may be achieved in as few as 10 generations.

As seen in each of the species groups of *Eucalanus*, differences in the integumental organs between species groups include features common to all members and those common to members comprising the group. Within a group differences tend to occur on or near the genital segment. Moreover, there is a general trend for differences to be more pronounced in the populations whose distributions are most extensive and bring them into contact with the largest number of other members within the species group. Thus, the pattern of integumental organs in *Eucalanus* show configurations that appear to have been shaped by character displacement (Brown and Wilson, 1956) in the broadest sense or what some (Blair, 1963; Littlejohn, 1965) have referred to as reinforcement. If so, integumental organs in copepods may play a significant role in the mating process.

CONCLUSIONS

1. This study provides unique and compelling evidence of the extensive information content applicable to systematics, phylogenetics, evolution, and population biology present in the integumental sensory and effector organs of planktonic copepods.

2. Integumental organs appearing on the body segments in *Eucalanus* are distributed in bilaterally symmetrical, serially homologous patterns that appear in both dorsal (tergal) and lateral (pleural) sets corresponding to the somites of the body. The organs fall into two basic groups: a) receptors that appear as hairs, pegs, or pits and b) integumental glands that communicate with pores on the surface of the exoskeleton. Within the set of a somite each designated site is constant in position and in morphological type of organ relative to the others comprising the set.

3. Analysis and survey of the gross morphology, distribution, and variation of these integumental organs was facilitated by a combination of techniques including a) digestion of internal tissues and intensive staining for light microscopy, b) clearing and integumental staining of intact specimens for light microscopy, and c) scanning electron microscopy. Processing of relatively large numbers of specimens was accomplished most efficiently using method a.

4. Comparative survey of integumental organs in 17 species recognized in this study as comprising the genus *Eucalanus* indicated that the numbers and arrangement of these structures reflect generic similarities, species group similarities, and individual species patterns, all

species but one pair being sufficiently distinctive in number and arrangement to be identifiable solely on the basis of integumental organs. Species grouped on the basis of integumental organs concur with groupings that utilize the seminal receptacle, segmentation of the abdomen and structure of the male fifth legs. In general, variation was negligible; about 80% of the sites in each species was observed in all specimens examined and an additional 10% appeared in from 80 to 99% of the specimens. The mean number of organs observed in samples of each population ranged from a low of 83 to a high of 135 in a combined total of 448 randomly selected specimens representing the 17 species in the genus.

5. Comparison of geographical relationships and number of integumental organs within each species group indicates that the species with the broadest geographical range is also the one with the most distinctive number or arrangement of integumental organs especially with respect to organs on the genital segment. The combination of species specificity, phylogenetic relationships, and geographical patterns associated with numbers and arrangement of organs indicate that the organs may function in prezygotic mating barriers within the genus.

6. Comparison of total length and number of integumental organs indicates that the two features are unrelated.

7. Variation in integumental organs in the circumglobal broadly tropical species *E. subtenuis* was found to have a strong geographical pattern indicating limited gene flow between the populations of the Eastern Tropical Pacific, the Indo-West Pacific, and the Atlantic Ocean. Some sets of organs were found to vary independently; others appeared to vary similarly providing evidence that the genetic control is complex. Their responses to selection pressures appear to vary sufficiently to warrant detailed study of *subtenuis* in relation to its closest cognate, *mucronatus*, within and outside of their region of co-occurrence.

8. Limited examination of males and copepodid stages III to V indicate that the integumental organs appear in the same numbers and arrangements that characterize the adult female except for structures that have not yet completed sexual maturation or are sexually dimorphic.

9. The attenuatus complex is revised on the basis of integumental organs and geographical distribution. Four biologically discrete populations are recognized, three being described as new species.

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DIFFERENTIAL BLOOD CELL COUNTS OF ATLANTIC HERRING, *CLUPEA HARENGUS HARENGUS*

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ABSTRACT

In differential blood counts of 200 herring, *Clupea harengus harengus*, the percentages of white cell types and immature erythrocytes in the blood were found to be different from those previously reported in the literature. Herring were sampled from February 1969 through July 1969 from the Boothbay Harbor, Maine, and Deer Island, New Brunswick, Canada, areas.

Immature erythrocytes in wild herring ranged from 6 to 38% with an average of 21; in captive herring they ranged from 2 to 22% with an average of 11. Thrombocytes were the most common type of leukocyte, followed in decreasing order by lymphocytes, neutrophils, basophils, and eosinophils in both captive and wild herring.

The percentage of each white cell type varied greatly between individual herring, but except in one instance, the mean percentage of each white cell type varied little between samples. One group of wild herring was unusual in that neutrophils averaged 21% of the leukocytes in contrast with an average of 4% neutrophils for three other wild samples and an average of 6.8% neutrophils for four captive samples.

The percentage of immature red cells varied widely between individual herring, but the mean percentage varied little between wild and captive herring within their respective categories.

The blood of herring has been studied at the Boothbay Harbor Laboratory to find physiological indicators of environmental stress that may help us determine causes of fluctuations in success of year classes. In previous published studies Naumov (1959) reported changes in the differential white cell counts of Atlantic herring, *Clupea harengus harengus*, from the Barents Sea and from the Greenland Sea in relation to the sexual cycle; Boyar (1962) reported no differences in the occurrence of blood cell types of Atlantic herring, *Clupea harengus harengus*, from the Gulf of Maine that related to length, or that offered any promise as an aging method. The differential white cell counts of herring I examined were different from those previously reported by Boyar and by Naumov. I shall report the results of my studies and discuss possible reasons for those differences.

MATERIALS AND METHODS

My analysis is based upon blood samples collected from wild herring obtained from commercial fishermen's catches and captive herring held in a tank at the Boothbay Harbor Laboratory. These data are shown in Tables 1 and 2.

All herring sampled from Boothbay Harbor were immature. Those from Deer Island were nonspawning mature fish and those from Eastport were 95% nonspawning mature fish and 5% immature fish. Captive herring were held in circular tanks having a capacity of 1,325 gallons. These tanks were supplied with unheated seawater which was pumped directly from the ocean. The water temperature was recorded at the site of capture in each instance.

Captive herring were fed a diet of canned cat food and commercial fish pellets. This diet was supplemented with natural food which entered the tanks through the water system. This natural food supply varied with the season; barnacle larvae were available in spring, and mollusk larvae were available in summer.

Slides were made from blood obtained by

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TABLE 1.—Wild herring (obtained from commercial fishermen's catches.)

Collection date (1969)	Source	No. of fish	Range	
			Length (cm)	Weight (g)
13 Mar.	Boothbay Harbor, Me.	34	11.6-19	9.4- 46.4
10 June	Eastport, Me.	32	14.5-30.4	18.0-214.5
8 July	Boothbay Harbor, Me.	45	12.5-18.2	12.7- 38.6
16 July	Deer Island, N.B., Can.	30	20 -24.6	56.5-119.3

TABLE 2.—Captive herring (held in a tank at the Boothbay Harbor Laboratory prior to collection of blood samples.)

Collection date (1969)	Months held captive	No. of fish	Range	
			Length (cm)	Weight (g)
25 Feb.	6	16	14 -17.2	14.2-29
24 Mar.	7	17	13.2-17.4	10.6-29.4
21 Apr.	8	18	14.3-17.7	14.9-33.1
23 June	10	8	13.1-18	14.1-34.7

direct heart puncture with a heparinized capillary tube. A small drop of blood from the capillary was placed on a microscope slide and the smear made. Slides were air-dried and stained by either the Wright's or Wright-Giemsa staining method. Distilled water was used as a diluent for the Wright's and Giemsa stains. The air-dried film was covered with Wright's stain for 1½ min, then an equal quantity of distilled water added and the film further stained for 3-4 min; then, either the diluted stain was flooded off with water and the slide dried, or the slide counterstained with diluted Giemsa for 20 min. Staining times varied slightly with different batches of Wright's stain. Each herring was measured for total length, weighed, sexed, marked, examined for gross parasitism, and frozen for reference in case abnormal blood properties were found. Cells were examined under oil immersion at 800 and 1,250 powers.

Differential counts were made of both red and white cells on an area of the slide where the cells were evenly distributed. A leukocyte differential count was made of a random selection of 100 leukocytes and listed under the following categories: lymphocytes, thrombocytes, neutrophils, eosinophils, or basophils. The range and mean percentage of each type of leukocyte present was calculated for each sample. An erythrocytic differential count was made of a random selection of 100 red cells and divided into mature or immature cells based upon their general morphology and staining properties. I classify herring erythrocytes in the peripheral blood according to the stage of development as erythroblasts, early polychromatics, mid-polychromatics, late polychromatics or mature cells. These terms were used by Lucas and Jamroz (1961) in describing the developmental stages of avian erythrocytes. The developmental stages for herring erythrocytes are described in Table 3. There are variations in individual herring in the size and shape between and within cell stages, and the amount of polychromasia present is the best indicator as to the stage to which the cell belongs. The primary morphological criteria I used in this paper were those of Boyar (1962). Additional references were consulted for a more definitive classification of cell types, to clarify the distinction of basophils from basophilic-staining immature erythrocytes, and to resolve confusion regarding the existence of monocytes in herring blood. These additional references were Catton (1951), Davidsohn and Nelson (1969), Jakowska (1956), Lucas and Jamroz (1961), Saunders (1968b), and Watson, Shechmeister, and Jackson (1963).

TABLE 3.—Erthrocytes in the peripheral blood of Atlantic herring, *Clupea harengus harengus*, according to the stage of development.

Stage	Description
Erythroblast	Round cell, similar in size to the early polychromatic. Has a dark blue staining cytoplasm with lightly stained spaces. The round purple-red staining nucleus is larger than that of the early polychromatic and takes up most of the cell. Erythroblasts are scarce in normal samples.
Early polychromatic	The smallest immature red cell that is normally seen in any quantity. Has a light blue to gray staining cytoplasm and appears round. The nucleus takes up most of the cell.
Mid-polychromatic	Round to slightly oval cell with a gray to light gray-orange staining cytoplasm. Cell is larger than the early polychromatic.
Late polychromatic	Slightly oval, has a larger cytoplasm and a smaller nucleus than the mid-polychromatic. The cytoplasm appears light orange-yellow.
Mature erythrocyte	Oval, has a slightly larger cytoplasm and a slightly smaller nucleus than the late polychromatic. The cytoplasm appears orange-yellow to reddish. Late polychromatic and mature erythrocytes have essentially the same appearance with Wright's and Wright-Giemsa stains.

RESULTS

Differential red and white cell counts are listed in Table 4. Blood cell measurements of all cells included in the differential counts are listed in Table 5.

The mean percentage of each white cell type varied greatly between individual herring, but except in one instance, the mean percentage for most white cell types varied little between samples. Thrombocytes were the most common leukocyte, followed in decreasing order by lymphocytes, neutrophils, basophils, and eosinophils in both wild and captive herring. One group of wild herring sampled on 8 July from Boothbay Harbor was unusual in that neutrophils averaged 21% of the leukocytes in contrast to an average of 4% neutrophils for three other wild samples and an average of 6.8% for captive herring. The herring from the 8 July sample were confined in the pocket of a stop seine overnight before being bled, in contrast to other wild herring that were bled immediately after the pocket was made in a purse seine (13 March) or in weirs (10 June and 16 July). The relative neutrophilia in the 8 July sample may be a result of the combination of being held overnight at relatively high water temperatures and crowded conditions. Temperature alone was evidently not the cause of relative neutrophilia in the July wild sample, for captive herring taken from nearly the same water temperature did not show relative neutrophilia.

Basophils and eosinophils were scarce in most herring examined, the greatest average (2% basophils) occurred in a wild sample from Eastport, Maine. Though one captive herring had 16% basophils, one wild herring from Eastport had 32% basophils, and another wild herring from Boothbay Harbor had 5% eosinophils and 17% basophils, no differences were found in those specimens in their red cell morphology or

TABLE 4.—Differential leukocyte and erythrocyte counts of wild and captive herring, *Clupea harengus harengus*, with the mean percentage and range (in parentheses) of each cell type.

Sample source and date	Water temp. (°C)	Number of herring	Type of leukocyte					Immature erythrocytes
			Thrombocytes	Lymphocytes	Neutrophils	Basophils	Eosinophils	
Wild:								
13 Mar. 1969 Boothbay Harbor, Maine	2.0	34	56.7 (33-75)	39.2 (23-58)	4.0 (0-13)	0.1 (0- 3)	0.0	19.1 (6-38)
10 June 1969 Eastport, Maine	7.7	32	53.3 (33-68)	40.8 (21-61)	3.8 (0-10)	2.0 (0-32)	0.1 (0-1)	21.2 (9-35)
8 July 1969 Boothbay Harbor, Maine	13.8	45	48.5 (21-79)	29.1 (9-62)	21.3 (8-47)	1.0 (0-17)	0.1 (0-5)	22.6 (12-33)
16 July 1969 Deer Island, N.B., Can.	9.8	30	62.7 (42-75)	31.8 (16-55)	4.5 (0-14)	0.9 (0-12)	0.1 (0-2)	19.0 (10-35)
All wild		141	54.6 (21-79)	34.7 (9-62)	9.6 (0-47)	1.0 (0-32)	0.1 (0-5)	20.7 (6-38)
Captive:								
25 Feb. 1969	1.3	16	80.2 (64-95)	13.0 (2-33)	6.6 (0-19)	0.1 (0- 1)	0.1 (0-2)	7.9 (2-19)
24 Mar. 1969	3.3	17	69.2 (29-89)	22.3 (9-51)	8.4 (0-20)	0.1 (0- 1)	0.0	11.2 (2-21)
21 Apr. 1969	4.9	18	67.8 (42-89)	26.3 (5-52)	4.6 (1-13)	1.1 (0-16)	0.2 (0-3)	12.3 (2-22)
23 June 1969	15.2	8	63.1 (35-76)	28.0 (18-48)	8.6 (1-17)	0.3 (0- 2)	0.0	13.2 (7-20)
All captives		59	70.9 (29-95)	21.8 (2-52)	6.8 (0-20)	0.4 (0-16)	0.1 (0-3)	10.9 (2-22)

TABLE 5.—Blood cell measurements in microns of wild Atlantic herring, *Clupea harengus harengus*, with the average size, standard deviation, and size range (in parentheses).

Cell type	Number of herring	Total number of cells measured	Cytosome		Nucleus	
			Length	Width	Length	Width
Erythrocytes:						
Mature RBC	8	200	10.7±0.9 (9.0-14.0)	7.8±0.6 (6.2-9.7)	4.6±0.5 (3.3-6.1)	2.9±0.2 (2.2-3.9)
Late polychromatic	6	150	10.4±0.8 (9.0-12.3)	7.6±0.6 (6.2-9.4)	4.8±0.4 (4.2-6.2)	2.9±0.2 (2.3-4.1)
Mid-polychromatic	6	150	9.5±0.7 (7.8-10.9)	7.1±0.7 (5.0-9.0)	5.0±0.5 (4.4-6.2)	3.0±0.2 (2.3-4.4)
Early polychromatic	6	150	8.2±0.7 (6.2-10.6)	7.1±0.7 (4.7-9.2)	4.9±0.5 (3.7-6.2)	3.4±0.4 (3.0-4.8)
Erythroblast	1	10	8.7±0.9 (7.0-9.4)	7.9±0.4 (7.5-8.6)	6.2±0.2 (5.5-6.2)	5.8±0.6 (4.7-6.2)
Leukocytes:						
Thrombocyte	3	100	8.9±0.9 (7.0-10.9)	4.4±0.5 (3.1-6.1)	7.2±0.6 (5.9-9.0)	3.5±0.5 (2.8-4.8)
Lymphocyte	2	100	7.7±0.9 (5.0-10.1)	7.4±0.8 (5.5-9.4)	6.4±0.6 (4.7-8.6)	6.1±0.6 (4.7-7.8)
Neutrophil	8	100	11.3±1.7 (7.6-17.2)	10.9±1.5 (6.2-15.6)	4.9±0.9 (2.2-6.2)	7.3±1.2 (3.6-10.9)
Basophil	6	100	12.4±1.6 (9.4-17.2)	12.0±1.2 (8.6-14.0)	5.1±1.2 (3.1-8.6)	6.6±1.4 (3.1-9.4)
Eosinophil	1	25	14.1±1.7 (10.1-17.2)	14.3±1.4 (12.5-17.2)	4.6±0.9 (3.1-6.2)	7.5±1.0 (6.2-9.4)

gross parasitism to distinguish them from other herring in their respective samples.

The mean percentage of immature erythrocytes varied widely between individual herring, but the mean percentage of immature erythrocytes varied little between samples of wild and captive herring within their respective categories. Wild herring had a greater percentage of immature erythrocytes at each sampling than did the herring held captive. Immature erythrocytes in wild herring ranged from 6 to 38% with an average of 21; in captive herring they ranged from 2 to 22% with an average of 11. As noted for other fish species (Catton, 1951; Hesser, 1960), films prepared from herring blood were characterized by the presence of more cellular debris and disintegrating cells than is usually found in films prepared from mammalian bloods. Erythroblasts, hemoblasts, and cells showing mitotic division were scarce in the peripheral blood of herring examined in this study.

DISCUSSION

The high variability in differential counts between individual herring is not unusual; such variability was noted in a number of vertebrate species (Altman and Dittmer, 1961:127-128). Lucas and Jamroz (1961) discussed the individual variability in blood values and the problems associated with this characteristic in avian species. Rooney, Roberts, and Dexter (1972), in differential counts of immature Atlantic salmon, found the most individual variability in thrombocytes, followed in decreasing order by lymphocytes and neutrophils.

Though I agree with Boyar (1962) in the general description of cell types in herring, my data differ markedly in the percentage of immature red cells in herring blood, in the percentage of white cell types present, and in the relative size of neutrophils in comparison to other white cell types. I found an average of 21% immature erythrocytes in 141 wild herring ranging in

length from 116 to 304 mm in my study, whereas Boyar reported immature erythrocytes and white cells combined constituted less than 3% of the total blood cells in the 85 wild herring ranging in length from 75 to 300 mm in his study.

Boyar (1962) reported neutrophils were much larger than other white cell types, with an average area twice that of the second largest cells, the eosinophils. However, in the herring I examined, the average area of neutrophils was larger than thrombocytes and lymphocytes, but smaller than basophils and eosinophils. The neutrophils in Boyar's line drawings of blood cell types have the appearance of cells that have been mechanically distorted. This flattening and spreading out would cause an increase in cell dimensions.

The average cell measurements in my studies are larger than those reported by Boyar, except in the case of neutrophils. Naumov (1959) reported ranges but not mean dimensions of leukocytes. My size range for neutrophils was similar to Naumov's, while the maximum sizes of individual lymphocytes and eosinophils were larger than reported by Naumov.

The total 8 July sample consisted of 76 herring. Five contained intracytoplasmic inclusions associated with erythrocytic degeneration (Sherburne, 1973). One herring in the total March wild sample, two herring in the total June captive sample, and two herring in the total 16 July wild sample contained erythrocytic inclusions. Though their white cell differentials did not differ markedly from other herring in their respective samples, the ten herring with inclusions are not included in this report.

Basophils were scarce and were not found in the leukocyte counts of 157 of the 200 herring in my study. Only 7 herring in my study had more than 5% basophils in their blood differentials. In contrast, Boyar (1962) reported basophils were the most abundant leukocyte in herring from brit 75 mm in length to sexually mature herring up to 300 mm. He reported basophils averaged 31% of the less than 3% cells other than mature erythrocytes (47% of the leukocytes) present in herring ranging in length from 101 to 200 mm, the predominant sizes of herring included in my study. Boyar also reported that basophils averaged from 18% to 56% of the leukocyte cell types in other size ranges of herring included in my study.

I have used the same staining method (Giemsa) used by Boyar and found no differences in the relative numbers of basophils compared with those I found using Wright's or Wright-Giemsa stains. Romer (1949) reported basophils are seldom found in fishes. Naumov (1959) found no basophils in sexually mature Murmansk (Atlantic) herring, *Clupea harengus harengus*, collected in 1938-39 from the Barents Sea and 1947 from the Greenland Sea. Saunders (1968a) found no basophils in blood smears of 49 species of teleost fishes from the Red Sea, and Saunders (1966) found basophils in the circulating blood of only 5 species out of 116 species of marine teleosts examined off Puerto Rico. The differences between Boyar's findings and my own may reflect environmental variations between the time of his study and my own. A more likely explanation is that Boyar confused certain basophilic staining immature erythrocytes with basophils. Small basophils are similar in size to basophilic staining immature erythrocytes, but in my slides these cell types were readily distinguished.

Thrombocytes were the most common leukocyte in my study; they constituted an average of 70% of the white cells in captive herring and 54% in wild herring. Boyar (1962) reported thrombocytes (spindle cells) made up 0 to 7% of the less than 3% cells other than mature erythrocytes present in his study. Saunders (1966, 1968a) reported thrombocytes were the most common leukocyte in the circulating blood of 116 species of marine teleosts from Puerto Rico and 49 species of teleost fishes from the Red Sea.

Boyar (1962) reported round, granular ghost cells averaged from 17 to 50% of the less than 3% cells other than mature erythrocytes present in his study. I also found round, anucleated cells occasionally in apparently normal herring, but most cells appeared finely vacuolated. Several blood smears from herring with intracytoplasmic inclusions associated with erythrocytic degeneration (Sherburne, 1973) had up to 50% round, anucleated cells present in the blood films. The anucleated cells appeared pale red with Wright's stain, were similar in size, and ranged from 9.4 x 9.4μ to 10.9 x 10.9μ. Some

of the cells appeared to show diffusion of nuclear material into the cytoplasm.

Naumov (1959) reported that the blood of sexually mature Murmansk (Atlantic) herring, *Clupea harengus harengus*, contained—in decreasing order of relative abundance—lymphocytes, monocytes, polymorphonuclear leukocytes, and eosinophils. Naumov, like many other authors, did not include thrombocytes in his differential counts.

In contrast to Naumov's report, neither Boyar (1962) nor I found monocytes in the Atlantic herring we examined. Jakowska (1956) discussed the confusion regarding the term monocyte, and because of the difficulty of recognizing monocytes with certainty, advised caution in including them as a separate category of teleost blood cell types. Catton (1951), Gardner and Yevich (1969), Hesser (1960), Romer (1949), Saunders (1966, 1968a) and Watson et al. (1963) did not report monocytes in teleost fish species they examined. Romer (1949) stated that monocytes, sometimes regarded as a separate category of white cells, appear to be merely large lymphocytes. I believe Naumov (1959) may have confused monocytes with large lymphocytes or neutrophils for the following reasons: Naumov reported lymphocytes in Atlantic herring ranged from 3.5 to 5.6μ, while monocytes ranged from 8.0 to 10.8μ. The lymphocytes in the herring I examined ranged from small (5μ) to large (10μ). Thus, perhaps Naumov's monocytes were actually large lymphocytes; however, he stated that during the process of regeneration of the gonads after spawning, there is an increasing quantity of monocytes and polymorphonuclear leukocytes in the blood evidently acting as phagocytes. Watson et al. (1963) stated that the neutrophil is a possible cause for some of the confusion regarding the existence of a monocyte within teleost blood, especially a neutrophil with a kidney-shaped nucleus. As the photographs in the translation of Naumov's report available to me are not clear and his monocytes and polymorphonuclear leukocytes have nearly the same range of dimensions (8.0 to 10.8μ and 8.5 to 14.4μ, respectively) perhaps his phagocytic monocytes were neutrophils.

Differential blood counts of herring fry 55-65 mm in total length, sampled in June and July 1971 from Boothbay Harbor, and mature herring 290-320 mm in total length, sampled 28 October 1972, northeast of Nantucket Shoals, confirm the findings of this study in that thrombocytes are the most common type of leukocyte in herring blood followed in decreasing order by lymphocytes, neutrophils, basophils and eosinophils.

This report provides a more accurate description of characteristic blood cell differentials found in Atlantic herring and provides a baseline for a systematic study of leukocyte differentials in physiologically stressed herring.

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A GENERAL LIFE HISTORY EXPLOITED POPULATION SIMULATOR WITH PANDALID SHRIMP AS AN EXAMPLE[1]

WILLIAM W. FOX, JR.[2]

ABSTRACT

A general life history population simulator, GXPOPS, with provisions to exploit any age sector of the population is presented. In addition to the usual fish life history pattern, the model allows simulation of random mating, sex-differential maturation, and stepwise growth found in many crustacean and some fish populations. GXPOPS provides for monthly calculations and all rates may be as general as month specific. The generality of the model is illustrated with an examination of closed season management strategies for a pandalid shrimp population.

The advent of the digital computer has allowed simulation modeling to become the current vogue within nearly all fields of science; fisheries is no exception. The computer has freed mathematically inclined scientists from being able to examine only equilibrium or cursory transitional states and from the need for expressing relations in neat closed analytical forms. Numerical integration schemes and the speed of computation have made possible the examination of large systems of differential equations with feedback mechanisms, both from deterministic and stochastic standpoints. Even the simplest self-regenerating population model of Beverton and Holt (1957), which may be regarded as a simulation model in that it has a feedback mechanism, is largely intractable for looking at transitional states and parameter variability without the aid of a computer.

Paulik (1969) gives a good review of simulation modeling in fisheries. He divided the modeling of fishery systems in an admittedly arbitrary way into two categories, management models and scientific models, depending on the manner in which a model is utilized. Management models are employed for decision making in evaluating or planning strategies for management purposes, while scientific models are constructed to help elicit certain basic knowledge of a biological system. The actual implementation of models in the two categories, however, should be similar in utilizing the model for planning, alternative evaluation, organization, and identifying sensitive areas of the system.

There are at least two fishery simulation models currently in existence which were designed to be generally applicable to most exploited populations. The most comprehensive is GAMES (Gales, 1972). This simulator has seven interacting sectors from the fish stock to the marketing of the final fish product, is modular in structure, and uses the most updated means of input/output. Unfortunately, GAMES is still in a state of development. The other simulator, POPSIM, was written by Walters (1969). POPSIM's major feature is an optimization routine for planning harvesting strategies for a number of harvesting periods. Both of these simulation models are easily adapted to the life history characteristics of fish populations which have been traditionally studied in fisheries science. However, the FORTRAN IV computer simulation model, GXPOPS, was written to allow additionally for the life history pattern of many crustaceans and some fishes that require actual copulation in reproduction and a sex-differentiated maturation schedule.

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MODEL STRUCTURE

A flow-chart of GXPOPS indicating the optional life history sectors is presented in Figure 1. Each sector is described by the equations below. The basic time period for calculations in GXPOPS is monthly with all processes summed or averaged annually. There are three output options: 1) annual summaries only, 2) monthly and annual summaries by age class, and 3) monthly listings by age class as well as monthly and annual summaries.

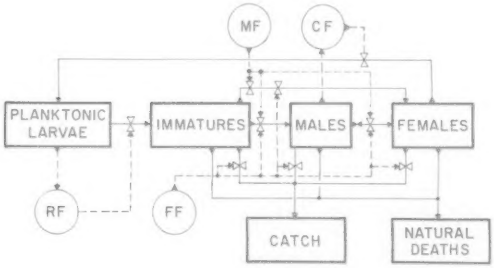

FIGURE 1.—Simplified flow chart of the computer program, GXPOPS. Boxes represent state variable compartments, solid lines represent material flows, dashed lines represent information flows, and circles represent regulatory functions: CF = copulation function, FF = fishing mortality function, MF = sex specific maturation function, and RF = recruitment function.

Mortality

Mortality may be age-specific on a monthly basis and is assumed to be representable by an exponential decline such that

$$N_{i,\,j+1} = N_{ij} e^{-Z_{ij}} \tag{1}$$

with

$$Z_{ij} = M_{ij} + A_{ij}F_{ij} \tag{2}$$

where N_{ij} is the number of animals belonging to the ith year class at the beginning of month j, M_{ij} is the instantaneous coefficient of natural mortality, A_{ij} is an availability multiplier, F_{ij} is the potential instantaneous coefficient of fishing mortality of a fully available year class, $i = 1. . . n$, and $j = 1. . . 12$. With natural and fishing mortality so general one can evaluate the effects of seasonal mortality patterns such as mass winter mortalities, closed seasons, etc. The coefficient A allows patterns of selectivity or seasonal availability, etc. to be incorporated. The average number alive of year class i during month j is given by

$$\bar{N}_{ij} = N_{ij}\,(1 - e^{-Z_{ij}})/Z_{ij}. \tag{3}$$

Growth

The growth in weight of the animals is represented by one of two options, the von Bertalanffy growth equation or a linear segmental growth curve as in POPSIM (Walters, 1969). The von Bertalanffy formulation is

$$w_{ij} = W_\infty\,[1 - e^{-K(12i + j - 13 - t_0)}]3 \tag{4}$$

where w_{ij} is the average weight of an individual in year class i at the beginning of the month j, and W_∞, K and t_0 are parameters of the von Bertalanffy growth equation. The segmental growth option is formulated as

$$w_{ij} = a + b\,\Delta t \tag{5}$$

where $a = w_{i,\,j-1}$, $b = (w_{ij} - w_{i,\,j-1})$ and $\Delta t = 1$. Using the segmental option, any shape growth curve may be approximated, including the stepwise growth pattern of crustaceans and many temperate fishes and mollusks.

Yield

Yield is computed monthly both in numbers and weight for each year class under either the von Bertalanffy or linear segmental growth option.

$$Y_{N_{ij}} = A_{ij}F_{ij}\bar{N}_{ij} \tag{6}$$

where Y_{Nij} is the yield in numbers. Under the von Bertalanffy growth option, the yield in weight, $Y_{w_{ij}}$, is computed as

$$Y_{w_{ij}} = A_{ij}F_{ij}N_{ij}W_{\infty}\sum_{u=0}^{3}\frac{\Omega_u e^{-uK(12i+j-13-t_0)}}{Z_{ij}+uK}$$

$$x\,[1-e^{-(Z_{ij}+uK)}] \qquad (7)$$

where $\Omega_u = 1, -3, 3, -1$, respectively. With the linear segmental growth option

$$Y_{w_{ij}} = Y_{N_{ij}}\{w_{ij} + (w_{ij+1} - w_{ij})$$

$$[1/Z_{ij} - 1/(e^{Z_{ij}} - 1)]\} \qquad (8)$$

Equations (7) and (8) are modified for monthly calculations from Beverton and Holt's (1957) equations 4.4 and 9.5 respectively.

Maturation

A maturity schedule of the sexes is necessary to compute several relationships associated with the reproductive sextor of GXPOPS. This is accomplished in the simulator with two vectors of age-specific values, one denoting the average fraction of mature males in each year class during the breeding season, ϕ_{mi}, and the other denoting the female fractions, ϕ_{fi}. The mean number of mature males, $\bar{N}_{m_j}$, and mean number of mature females, $\bar{N}_{f_j}$, during month j of the spawning season are

$$\bar{N}_{m_j} = \sum_{i=1}^{n}\phi_{mi}N_{ij}\,(1-e^{-Z_{ij}})/Z_{ij} \qquad (9)$$

and

$$\bar{N}_{f_j} = \sum_{i=1}^{n}\phi_{fi}N_{ij}\,(1-e^{-Z_{ij}})/Z_{ij} \qquad (10)$$

with

$$s_j = \bar{N}_{m_j}/\bar{N}_{f_j}, \qquad (11)$$

where s_j is the mean monthly sex ratio. The mean sex ratio for the breeding season is given by

$$\bar{s} = [\sum_{j=t_s}^{t'_s} s_j]/(t'_s - t_s + 1) \qquad (12)$$

where t_s and t'_s are respectively the months that breeding begins and ends.

The maturation fractions, ϕ, are assumed to be constants in the present version of GXPOPS. It is possible that the ϕ may be density-dependent in certain populations. One can investigate the effect of differences in ϕ at equilibrium with the current version of GXPOPS, but it would be a simple matter to reprogram GXPOPS to examine the consequences of any functional hypotheses.

Reproduction

The major components of the reproduction sector of GXPOPS are copulation, egg-carrying (ovigerous period), and hatching. For the common spawing characteristics of freely casting both spermatozoa and eggs, the copulation and ovigerous period sector may be bypassed.

The traditional concept of fertilization success in fisheries population dynamics, excluding the salmonids, is described by Beverton and Holt (1957, p. 61) as:

> . . . if there is free liberation of gametes, with spermatozoa greatly in excess of eggs, and especially if the percentage of successful fertilisations is fairly high, then the number of fertilised eggs would tend to be a constant fraction of the numbers laid. In addition, a large spawning population would tend to distribute eggs over a rather wider area than a small one, so that the number of gametes per unit volume, which in such a situation determines the rate of fertilisation, would not be expected to change much.

Copulation is one mode of ensuring the fertilization of eggs in sexual reproduction. The success of fertilization, therefore, depends on the copulation rate which is at least some function of the sex ratio and density of the mature population. Beverton and Holt recognized this may be the case for a lobster population, in which copulation occurs.

Copulation is a part of reproduction in most commercially exploited crustaceans, and some fishes. With the exception of salmonid studies, where a form of pseudocopulation occurs, population dynamics studies of commercial fisheries have ignored the effects of exploitation on the rate of copulation. Conway (1969) presents the most extensive quantitative treatment of reproduction in insects, whose copulation parallels

that of many crustaceans. He recognizes three types of mathematical models for representing reproduction: 1) derivations from the Lotka-Volterra equations, 2) empirical models (essentially multiple regressions from data sets with a number of variables), and 3) structural models of the causal mechanisms likely to be involved.

Derivations from the Lotka-Volterra equations assume that if mating is random, then the rate of change of copulated females is proportional to the expected rate of contact per female times the number of uncopulated females. The rate of contact per female is assumed to be proportional to the number of males, giving

$$dN_f^*/dt = k_c N_m (N_f - N_f^*) \tag{13}$$

where * denotes copulated females and k_c is the coefficient of copulation. The copulation coefficient may be thought of as consisting of two multipliers — the instantaneous coefficient of males contacting females at random and the fraction of these encounters that result in copulation. Equation 13 has the solution

$$N_f^* = N_f(1 - e^{-k_c N_m}) \tag{14a}$$

or

$$p = (1 - e^{-k_c N_m}) \tag{14b}$$

where p is the fraction of mature females that, at the end of the breeding season (scaled to be of one unit length for convenience), have been copulated. Equation (14b) may also be derived probabilistically by assuming the number of copulations is Poisson distributed such that k_c is the mean rate of contact resulting in copulation per male, then

$$P_r\,[x \text{ copulations}] = e^{-k_c N_m} \frac{(k_c N_m)^x}{x!}$$

with equation (14b), therefore, expressing the probability that at least one copulation per female has occurred in one unit of time (Klomp, Montfort, and Tammes, 1964 [cited in Conway, 1969]). This assumes that the population is not aggregated but is randomly distributed over the breeding grounds regardless of the size of the population. Philip (1957) has also derived equation (14b) under slightly different circumstances. Writing equation (14a) in terms of the sex ratio (males: females), s, and total mature population, N_a, we have

$$N_f^* = \left(\frac{1}{1+s}\right) N_a \left[1 - e^{-k_c \left(\frac{s}{1+s}\right) N_a}\right]. \tag{15}$$

Therefore, as the total mature population decreases, or as the sex ratio increases, the number of females being copulated with decrease under this model for reasonable values of s in the virgin state.

With the aid of equation (15) one can easily follow the reasoning of Beverton's and Holt's conclusions for large, long-lived fish populations with essentially a constant sex ratio. The maximum sustainable average yield (MSAY) in these populations is likely to occur at relatively low rates of fishing, hence there would be only a small reduction in population size from the virgin state. If k_c were high, then the reduction in N_f^* would be negligible. On the other hand, if the population is short-lived, the MSAY is likely to occur at a relatively lower population level. If fishing also increases the sex ratio, the deleterious effects on the size of N_f^* are compounded.

Equation (13) may be extended to become more realistic for a multiage population under exploitation. Often the mortality during breeding is neglected; however, exploitation may increase the mortality significantly and the breeding season may be protracted. Therefore, with the additional assumption that males make no distinction between year classes of females, for any year class i during month j

$$dN_{fi}^*/dt = k_c N_m(t)\,[N_{fi}(t) - N_{fi}^*(t)\,] - Z_i N_{fi}^* \tag{16}$$

where

$$N_m(t) = \sum_{i=1}^{n} \phi_{mi} N_{ij} e^{-Z_{ij} t} \tag{17}$$

and

$$N_{fi}(t) = \sum_{i=1}^{n} \phi_{fi} N_{ij} e^{-Z_{ij} t} \tag{18}$$

Rewriting equation (16) in terms of the ratio of

copulated females to total mature females, $p(t)$, giving

$$dp(t)/dt = k_c \sum_{i=1}^{n} \phi_{mi} N_{ij} e^{-Z_{ij}t} [1 - p(t)], \quad (19)$$

the solution obtained is

$$p_j = [1 - e^{-k_c \sum_{i=1}^{n} \phi_{mi} N_{ij} (1 - e^{-Z_{ij}})/Z_{ij}}] \quad (20)$$

with $t = (0, 1)$ months and $p_0 = 0$. Equation (20) may be further simplified by substitution from equation (9) to give

$$p_j = [1 - e^{-k_c \bar{N}_{mj}}]. \quad (21)$$

Therefore, the fraction of the females in any year class that are copulated is the same for all year classes *provided that* k_c *is not age specific*. Given the fraction copulated in the previous month, p_{j-1} [where $p_{t_s - 1} = 0$], the fraction copulated at the end of the month j is

$$p_j = [1 - (1 - p_{j-1}) e^{-k_c \bar{N}_{mj}}]. \quad (22)$$

The total number of females in the population bearing fertile eggs at the end of the breeding season is then

$$N^*_{ft'_s} = p_{t'_s} \sum_{i=1}^{n} \phi_{f_i} N_{it'_s}, \quad (23)$$

further assuming that one copulation results in fertilization.

Recounting the assumptions implicit in the simple model, equation (23), they are:

1. The instantaneous copulation rate per female is linear and proportional to the number of males.
2. The copulation coefficient is independent of the age of the males and females.
3. The copulation coefficient is independent of population size.
4. A single copulation results in fertilization.
5. Multiple copulations, if they occur, do not alter the fraction of each egg clutch that is fertilized from the first copulation.

In developing a reproduction model for insects, Conway (1969) criticized the first assumption as being unrealistic. Empirical evidence and biological induction suggest that the copulation rate should be concave downwards, rising to a maximum at some intermediate density and declining at very high densities owing to interference. Conway (1969) dismissed the second type of models (empirical) as lacking generality for a critical examination of reproduction, and developed three structural models based on nearest neighbor distances. Given the population size, density, and sex ratio, four parameters are contained in his models as compared with only one for the simple model. Conway fits each of his models to data obtained from the literature on insects. The fits he obtained are hardly remarkable considering that four parameters were estimated, and a number given, for only eight points. However, the fits are an indication of the flexibility and possible validity of Conway's structural concepts—especially since an irregularity in the data with biological significance was predicted with the fitted model. The decline in copulation rate in the data, however, occurs at very high population densities. The major use of GXPOPS will likely be for examining the dynamics of populations under exploitation, hence at less than virgin population densities. Also, since the two data sets given by Conway are adequately described by a straight line for the observations at population densities before the decline in copulation rate occurred, and lacking other empirical evidence to the contrary, equation (22) was adopted as the copulation model in GXPOPS.

Many exploited animals carry their fertilized eggs so that the number of eggs reaching the hatching period is intimately tied to the survival of the females during the ovigerous period. If it is assumed that all female mortality results in the loss of the eggs as well, then the number of copulated females reaching the hatching period is given by

$$N^*_{ft'_h} = p_{t'_s} \sum_{i=1}^{n} \phi_{fi} N_{it_h} \quad (24)$$

where t_h is the time at hatching. Instantaneous

hatching is assumed, so t_h represents the mean hatching time.

Individual fecundity (eggs per female) is usually correlated with the size of the individual. Many plots of fecundity on length appear to be concave upward, which indicates that fecundity is closely proportional to the weight of the individual. In order to be more useful generally, however, fecundity in GXPOPS is represented by a vector of mean viable eggs per female at hatching by age class, λ_i, such that the total number of larvae hatched, L_h, is given by

$$L_h = p_{t'_s} \sum_{i=1}^{n} \lambda_i \phi f_i N_{it_h}. \quad (25)$$

Recruitment

Any equilibrium point achieved with the population model as now formulated is likely to be unstable, such that with a sustained increase or decrease in mortality the population will decrease to extinction or increase to infinite size. Most successful natural populations are believed to achieve equilibrium through any of a number of homeostatic mechanisms associated with density-dependent reproduction or mortality. One such mechanism already mentioned is a decrease in copulation rate at high densities. Others include a lack or destruction of oviposition sites at high densities as in insects or salmonid fishes, an overutilization or competition for a fixed food supply, cannibalism, predator-prey interactions, etc. The usual mode of population regulation assumed in fisheries studies is through density-dependent early stage (or larval) mortality. Treatises on this subject can be found in Ricker (1954, 1958) and Beverton and Holt (1957).

Two models have been widely used in fishery population dynamics; GXPOPS allows the selection of one or the other. The first model, owing to Beverton and Holt (1957), states that the simplest assumption one can make is that the larval mortality coefficient can be expressed as a simple linear function of larval population size

$$dL_t/dt = -(\mu_1 + \mu_2 L_t) L_t \quad (26)$$

where μ_1 and μ_2 are the density-independent and density-dependent larval mortality coefficients. Equation (26) integrates to

$$L_j = [\mu_2/\mu_1 (e^{\mu_1} - 1) + e^{\mu_1} /L_{j-1}]^{-1} \quad (27)$$

for the survival of larvae from month $j - 1$ to j. Collecting the constants we have

$$L_j = 1/(\alpha_1 + \alpha_2/L_{j-1}),$$

or

$$L_{h+t_r} = 1/(\alpha_1 \sum_{r=0}^{t_r - 1} \alpha_2^r + \alpha_2^{t_r}/L_h) \quad (28)$$

for t_r months of larval existence. Equation (28) is a concave downward function that increases monotonically with L_j for a constant period of larval existence and it approaches an asymptote of $\sum_{r=0}^{t_r - 1} \alpha_2^r/\alpha_1$ at an increasing rate as α_2 increases.

The second model, owing to Ricker (1954, 1958), simply assumes that the density-dependent coefficient, μ_2, may operate only until some critical size is reached and that the time to attain this critical size may be proportional to the size of the larval population at hatching, L_h, which gives

$$dL_t/dt = -(\mu_1 + \mu_2 L_h) L_t$$

or on integrating

$$L_{h+t_r} = L_h e^{-(\mu_1 t_r + \mu_2 L_h)} \quad (29)$$

for t_r months of larval existence. Equation (29) is also concave downwards, but monotonically increases to a maximum at $L_h = 1/\mu_2$, and then monotonically decreases approaching zero as L_h becomes infinite.

Both equations (28) and (29) allow a population to achieve stability over a range of sustained mortality rates. Equation (29), additionally, will produce oscillations in the population (Beverton and Holt, 1957), the criteria for which are given by Paulik and Greenough (1966).

Constant recruitment of size $1/\alpha_1$ may be simulated with GXPOPS by selecting equation (28) and setting $\alpha_2 = 0$.

Timing in the Simulator

Reference in this study is made to a year divided into 12 mo because the reproductive cycles of many exploited fish populations are annual. It is just as easy to consider the "year" as a reproductive cycle (16 days, 3 yr, etc.) divided into 12 time periods of equal length.

The conventional notation, for numbering timestream entities, is for the initial or first instance to be denoted as 0. The computer, however, begins with 1 in executing "DO" loops, etc., therefore, the ordinal numbering system is used in GXPOPS. The first month and year are denoted as 1, as are the initial numbers and yields of the first month and year, and the young of the year. The simulator takes the hatching time, t_h, as time 1 (i.e., $L_h = L_1$) and the year is carried on a biological fiscal basis. For example, if hatching occurs on April 1, recruitment to the main population on July 1 of the first year of life, and breeding begins October 1 and ends December 1; then

$$t_h = 1,\ t_r = 3,\ t_s = 7, \text{ and } t_s' = 8,$$

respectively. If recruitment does not occur until July 1 of the third year of life, then $t_r = 27$.

EXAMPLE: A PANDALID SHRIMP POPULATION

GXPOPS was designed to be useful for examining the responses of many life history patterns to exploitation. The impetus, however, was to examine the response to exploitation of a pandalid shrimp life history (Fox, 1972). Pandalid shrimps are protandric hermaphrodites—i.e., individuals mature as males but later transform to function as females (Berkeley, 1930), fertilization is accomplished through copulation, the females carry fertilized eggs 3-9 mo until hatching, and they exhibit pronounced stepwise growth. While the extensive simulation studies investigating the effects and management implications of all sectors of the pandalid shrimp model will be published subsequently, one particular study of the effect of season length on the simulated fishery is useful for illustrating the utility of GXPOPS.

Table 1 contains the parameters of the simulated pandalid shrimp population which 1) consists of six year classes, 2) is fully recruited to the fishable population during the third year of life (at 2 yr old), 3) breeds over 2 mo, 4) carries its eggs 5½ mo until hatching, 5) recruits to the main population during the fourth month of life (3 mo after hatching), 6) matures as males during the third year of life (at 2 yr old), and 7) transforms into females during the fourth year of life (at 3 yr old). The stepwise growth in weight is given in Figure 2.

Exploiting the simulated pandalid shrimp produced the relationship between equilibrium yield and fishing effort (= instantaneous fishing mortality coefficient since the catchability coefficient was assumed to be 1.0) given in Figure 3. An equilibrium yield was achieved with fishing effort up to 1.4, with the maximum equilibrium yield occurring at about 1.0. Fishing above a level of 1.4 did not result in equilibrium within 25 yr of simulated fishing, and continued fishing somewhere between 1.4 and 2.0 would eventually result in extinguishing the population. By not including the effect of random mating (copulation), i.e., $k_c = \infty$, the simulated population achieved equilibrium out to nearly $F = 1.8$ (Fox, 1972). This exhibits some need for considering the implications of copulation success in evaluating management alternatives.

The equilibrium yields given in Figure 3 are for an annual pandalid shrimp fishery. Several states, however, have closed seasons during that part of the year when females are carrying fertilized eggs — ovigerous period — (Dahlstrom, 1970). For the simulated pandalid shrimp population, the ovigerous period lasts 6 mo (months 7-12). It is of interest to compare the results of the closed ovigerous season strategy with other possible season lengths, all beginning subsequent to hatching and running continuously until reaching the closed season.

TABLE 1.—Parameters of the simulated pandalid shrimp population.

Parameter	Symbol	Value
1. Number of year classes	n	6 (i = 1-6)
2. Instantaneous natural mortality coefficient	M_{ij}	0.06 (for all i and j)
3. Availability multipliers	A_{ij}	0.0 (for $i \leq 3$) 1.0 (for $i \geq 3$)
4. Month breeding begins	t_s	7
5. Month breeding ends	t'_s	8
6. Year of first maturity	t_m	3
7. Age (mo) at first recruitment	$t_r + 1$	4
8. Copulation coefficient	k_c	10^{-9}
9. Recruitment parameters of the Beverton and Holt model	α_1 α_2	3.2851×10^{-11} 1.01
10. Fecundity coefficients	λ_i	0.0 (for i = 1-3) 1314 (for i = 4) 1679 (for i = 5) 1997 (for i = 6)
11. Male maturity fractions	ϕ_{mi}	0.0 for i = 1, 2 and 4-6 1.0 for i = 3
12. Female maturity fractions	ϕ_{fi}	0.0 for i = 1-3 1.0 for i = 4-6

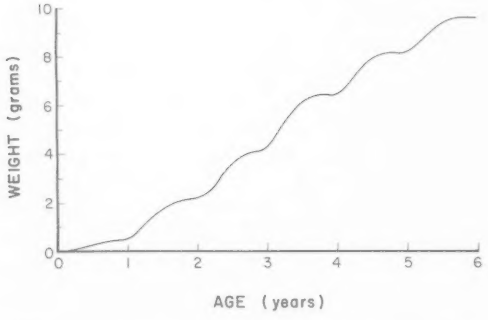

FIGURE 2.—Arbitrary growth curve exhibiting the stepwise growth pattern of pandalid shrimps.

The simulated pandalid shrimp population was fished for six different season lengths, from 12 to 2 mo after the hatching period (Table 2). The maximum equilibrium yield for each season length occurred with an *annual* fishing mortality coefficient, F, of 1.0. This means that the monthly fishing effort must increase proportionally to the inverse of the season length to obtain the maximum equilibrium yield (column 2, Table 2). Of those seasons simulated, the greatest equilibrium yield and catch per unit effort were obtained with the 8-mo season (columns 3 and 4, Table 2). Compared with an annual fishery, however, the 8-mo season resulted in a 5% decrease in the average weight of a shrimp in the catch (column 5, Table 2). The 6-mo season (closure during the breeding, ovigerous, and hatching periods) was only slightly less than the 8-mo season in yield and catch per unit effort, but it was better than the annual fishery. However, there was an 11%

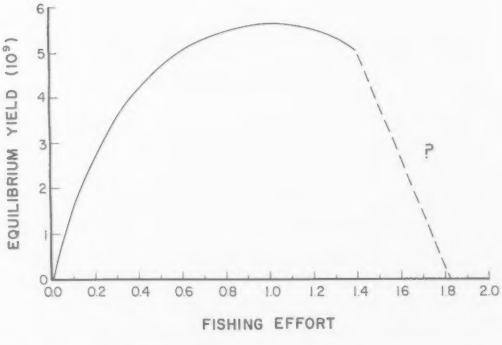

FIGURE 3.—Relationship between equilibrium yield and fishing effort for the simulated pandalid shrimp population. Dashed line represents nonequilibrium region.

TABLE 2.—Effect of season length, beginning subsequent to hatching, on maximum equilibrium yield and allied fishery parameters for the simulated pandalid shrimp population.

(1) Season length (months)	(2) Monthly fishing effort	(3) Season yield in weight	(4) Average monthly catch/effort	(5) Average individual weight	(6) Breeding success (percent)
12	1.0	5.60×10^9	0.467×10^9	3.7	85.5
10	1.2	5.68×10^9	0.474×10^9	3.6	82.0
8	1.5	5.70×10^9	0.475×10^9	3.5	76.1
6	2.0	5.67×10^9	0.472×10^9	3.3	71.3
4	3.0	5.63×10^9	0.469×10^9	3.1	71.3
2	6.0	5.57×10^9	0.464×10^9	2.9	71.3

decrease in average weight as compared to the annual fishery. The breeding success, defined as the fraction of available eggs which are fertilized, declined with the season length until a 6-mo season was reached.

An unknown factor not programmed into the simulation model, however, is the effect of trawling on the behavior of the shrimp during breeding or on the possibility of causing dislodgement of the egg clutches and a subsequent higher mortality rate. In view of these uncertainties, the adoption of a 6-mo season from hatching to the onset of breeding, as several states have, appears to be a biologically prudent approach for a natural population similar to the simulated population. The 6-mo season is only slightly lower in maximum equilibrium yield, catch per unit effort, and average size than the optimal 8-mo season, but is better than the annual fishery in the first two categories. The actual implementation of a 6-mo season on an annual fishery, however, would have to weigh socioeconomic factors because the maximum yield is obtained with twice the amount of fishing effort per month as compared with the annual season. If the fishery were only able, at the time of adopting the closed season, to exert a monthly effort of 1.0, the expected seasonal equilibrium yield is about 10-15% less than that for the annual fishery, but the expected equilibrium mean monthly catch per unit effort would increase 70-80%. The latter should provide a substantial increase in the economic standard of an average fisherman, provided that he has an alternative means of investment for the 6-mo closed season which would provide a sufficient return. The simulation model can be used also to evaluate the expected transitional states from an annual fishery to a seasonal closure fishery as well as the expected equilibrium results discussed here. A socioeconomically feasible strategy, then, may be determined given the current state of the fishery.

PROGRAM AVAILABILITY

A listing and card set-up documentation for program GXPOPS are available on request from the author.

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CHARACTERIZATION OF THE OPTIMUM DATA ACQUISITION AND MANAGEMENT OF A SALMON FISHERY AS A STOCHASTIC DYNAMIC PROGRAM[1]

GARY E. LORD[2]

ABSTRACT

The optimum data acquisition and management of a typical Bristol Bay sockeye salmon fishery have been expressed as a problem in statistical decision theory. Optimality has been defined as that set of sequential decision rules that minimizes the Bayes risk over the duration of the run. Economic losses or costs are ascribed to acquisition of catch and escapement data in such a manner that an optimal data acquisition scheme can be defined in addition to defining the set of optimal management strategies.

The management and inshore harvesting of salmon stocks characteristically consist of several interrelated phases. Stock assessment and run profiling are of importance both to the management personnel and to segments of the industry in planning their respective operations. Prior knowledge of the run size and time profile is useful in the preliminary planning of a management strategy that will in some way permit the escapement of the desired number of spawners. Similarly, such information also serves the industry in planning the level of its anticipated activities (Mathews, 1967). The theoretical investigation described here was motivated by specific consideration of the data gathering and management schemes currently applied in the Bristol Bay sockeye salmon fisheries. However, the formulation is relatively abstract and of sufficient generality so that, properly interpreted, it may apply to a variety of fishery situations which are evolutionary or time varying in nature. Indeed, it is this dynamic aspect of the problem that is at once the crucial feature of the analysis and also the principal source of analytical and computational difficulty.

Rothschild and Balsiger (1971) treated the optimum management of the Kvichak fishery of Bristol Bay as a problem in linear programming in which the various entities comprising the run could be optimally allocated, subject to various constraints on escapement, sex ratios, etc., over the duration of the run. Optimality was chosen as that set of allocation rules which maximized the economic return, expressed as a linear objective function, subject to the satisfaction of a set of linear inequality constraints. This formulation and solution as a linear program are particularly powerful since the solution, easily obtained by standard techniques, is particularly rich in interpretive detail.

The formulation and solution as a linear program suffer from several disadvantages, as Rothschild and Balsiger noted in their paper. First, the solution is deterministic in that it assumes precise knowledge of the run size and its time profile. In actual practice, although there is considerable investment in stock assessment and run forecasting, the resulting estimates are subject to considerable variation. Second, not all of the constraints are "firm," i.e., inviolable. This applies especially to the escapement. Presumably a unique optimum escapement for each actual realization of the run exists, but it is not necessarily imperative that this escapement be attained. Instead it may be assumed that an escapement below the optimum is accompanied by some economic loss, suitably discounted, for the diminished future returns. Similarly, an excessive escapement will result in a loss due to the decreased catch and, if in the right-hand tail of a dome-shaped (Ricker

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type) spawner-return curve, there will be an additional loss due to decreased returns. Finally, the linear programming formulation is essentially static although Hillier and Lieberman (1967) discuss certain techniques that are applicable to a limited class of stochastic and dynamic allocation problems. However, the only such technique that would be readily applicable to the fishery management case is chance constrained programming in which the admissibility of "soft" constraints, i.e., constraints which may be violated with certain allowable probabilities, is permitted.

In the subsequent analysis an attempt is made to simulate directly the inherently stochastic and dynamic nature of the management of a typical salmon fishery. A brief discussion of the assumptions made as well as a comparison with the linear programming formulation of Rothschild and Balsiger will also be given. This comparison of methods should be considered to be somewhat subjective and reflects, to a certain extent, the author's own opinions and predilections. The interested reader may be able to arrive at more meaningful comparisons and conclusions after studying the respective analyses in more detail.

We will assume here gear of fixed selectivity with regard to sexes and year classes. This corresponds to the status quo with respect to Bristol Bay although Rothschild and Balsiger showed that an optimum allocation among the various entities comprising the run was economically advantageous, particularly in the case of altered sex ratios. The fixed selectivity assumption, which results in an allocation based only on total numbers of fish, is made principally in the interests of tractability although it is possible to generalize the loss functions and probability densities to include the various individual entities.

Hillier and Lieberman list and discuss the basic features which serve to characterize dynamic programming problems. The principal characteristics will be repeated here, paraphrased slightly, and it will be shown here and in the subsequent analysis that the salmon fishery management problem conforms quite naturally to the class of problems for which dynamic programming is applicable.

1) The problem can be divided into stages with a policy decision required at each stage. This is obviously the case in Bristol Bay where the stages consist of discrete fishing periods, for each of which a management decision must be made. Discreteness is not an essential feature, however, since continuous time allocation problems may also be treated by dynamic programming techniques.
2) Each stage has associated with it a (possibly infinite) number of states. The state of the system is somewhat difficult to characterize precisely. It will be sufficient to treat the state of the system, in this case the salmon fishery, at the start of any stage as reflecting the true state of nature, e.g., run size, time profile, migration patterns, etc., as well as the effects of all previous policy decisions through the preceding time period. Closely related is:
3) The effect of the policy decision at each stage is to transform the current state into a state associated with the next stage. We will generalize this slightly to include sequentially acquired data as an additional quantity serving to characterize the state of the system and the transformation from one state to the next. The remainder of the characterizing features enumerated by Hillier and Lieberman are related to the very fundamental "Principle of Optimality," the statement and discussion of which will will be deferred until the section on Discussion.

The close correspondence of the concepts of dynamic programming, and also the closely related sequential statistical decision theory, to the problem of salmon fishery management suggests that together they provide potentially powerful tools for the description and simulation of such processes. A caveat is appropriate here, however. In general there will be the loss of a considerable portion of the economic "fine structure" of the problem, particularly in comparison with the solution as a linear program. The solution of the linear programming primal

and its dual allows one to make inferences beyond simply the attainment of the optimum. This was emphasized adequately by Rothschild and Balsiger in their identification and discussion of the various shadow prices, etc. A more serious reservation concerns the very serious analytical and computational difficulties to be anticipated. It is a truism of dynamic programming that many more problems may be formulated than may be solved, and it is not at all certain at present whether the salmon fisheries problem falls into the soluble category. Thus, the present discussion will be confined to the presentation of the theory, which is self-contained. The very difficult problems of formulation of the loss functions and the selection of optimum decision rules will be the subject of subsequent investigations.

THEORY

It is helpful to think of the salmon run, its assessment, and its management as evolutionary processes in time. Prior to the start of fishing the management biologist has at his disposal certain prior information, such as preseason forecasts, on which to base his early management strategy. As the run proceeds, additional data are gathered so that, as his knowledge of the true state of nature increases, he may modify his strategy to conform more closely to the optimum strategy. This will now be developed more formally.

Assume that the entire run occurs over a total of m discrete nonoverlapping time intervals. If n_i is the number of fish entering the fishery on the ith day then the total run size, N_{tot}, is given by

$$N_{\text{tot}} = \sum_{i=1}^{m} n_i. \tag{1}$$

Define a parameter vector $\underset{\sim}{\theta}$, of arbitrary dimension, that is assumed to characterize all relevant details of the run. As a specific example, we could define $\underset{\sim}{\theta}$ of the m-dimensional vector $(n_1, n_2, \ldots n_m)$, i.e., the ith component of $\underset{\sim}{\theta}$ is the number of fish entering the fishery on the ith day. More generally, we can leave $\underset{\sim}{\theta}$ arbitrary and write $n_i = n_i(\underset{\sim}{\theta})$. For each known $\underset{\sim}{\theta}$ there exists some known set of optimum allocation rules $\eta_i(\underset{\sim}{\theta})(i = 1, \ldots m)$ where η_i is the optimum fraction of the fish to be allocated to the catch on the ith day. For example, the linear programming formulation of Rothschild and Balsiger provided a set of optimum allocation rules based on a fixed total run size and a two parameter time profile proposed by Royce (1965).

Let D be a finite set of decision rules and let δ_i, a member of D, be the decision adopted on the ith day. Typically the set D consists of such management decisions as fishery opening or closing, fishing area limitations, etc. For each δ_i there will be an actual allocation $\hat{\eta}_i$ where, in general, both η_i and $\hat{\eta}_i$ will be random variables. The former will depend on the true (unknown) state of nature, $\underset{\sim}{\theta}$, while the latter will also be a random function of $\underset{\sim}{\theta}$ as well as of the decision taken, δ_i. As the actual and optimum allocations differ, various economic losses will be assumed to accrue, and the average or expected loss will be these losses averaged over all possible outcomes. This will be developed more formally after considering the various loss functions.

We may postulate the existence of an overall loss function that reflects economic losses from all sources. For our purposes we will consider the loss as arising only from 1) the cost of data acquisition, 2) the catch, and 3) the escapement. Since the catch and the escapement are complementary quantities, their sum comprising the total run, we could consider either one individually as is done in a subsequent example using the Ricker (1958) spawner-return relation. However, an individual treatment of each permits the separate discussion of loss functions that are linear, additive, and separable, as for the catch, and those which are nonlinear and not additive, as will be postulated for the escapement.

First consider the cost of data acquisition. Generally, the sampling schemes to be used and the level of effort for each are selected prior to the run. There may be in-season variations, such as occasional stream surveys, etc. but the cost associated with these is much less than that allocated prior to the run. We denote the experimental design symbolically by ζ and, in line with the above argument, there is

associated with ζ some fixed cost $C(\zeta)$. The quanitity ζ, which is an abstract designation of the experimental design, will also appear as a conditioning quantity when we consider the various probability density functions associated with the sampled quantities, i.e., the distribution of the sample estimates will depend on, among other things, the manner in which the data are acquired.

Next is the loss associated with the catch. Consider the start of the kth time period where $1 \leq k \leq m$ but otherwise arbitrary. If the economic value of the catch is assumed to be linear and additive, we may write

$$L_X(k) = \sum_{i=1}^{k-1} v_i [\eta_i(\underset{\sim}{\theta}) - \hat{\eta}_i] n_i(\underset{\sim}{\theta}) \qquad (2)$$

as the loss through the (k - 1)st time period for the catch.[3] Here v_i is the unit value of the fish for the ith interval. Note that if $\hat{\eta}_i$ exceeds η_i, i.e., the actual catch exceeds the optimum catch, the loss function is negative and becomes a gain function. However, this apparent benefit must be offset by the loss associated with the corresponding decreased escapement. If this were not the case, then this would not be the correct optimum since any departure from the optimum must result in a nonnegative incremental loss.

Finally consider the loss function for the escapement. This function cannot be considered to be linear or additive since the average number of returns per unit of spawners escaping on any particular day will be a function primarily of the final value of the total escapement. This is a consequence of the fact that late spawners may interfere with the redds of the earlier arrivals and thus diminish the returns for this group. Also, excessive escapement may lead to increased competition for food among the fry to the general detriment of the population as a whole. Thus, to a first approximation, the loss function for the escapement depends only on the final values of the actual and optimum escapements. Symbolically this may be written as

$$L_E(m) = \phi(E, \hat{E}) \qquad (3)$$

where

$$E = \sum_{i=1}^{m} (1 - \eta_i) n_i(\underset{\sim}{\theta}) \qquad (4a)$$

is the optimum total escapement while

$$\hat{E} = \sum_{i=1}^{m} (1 - \hat{\eta}_i) n_i(\underset{\sim}{\theta}) \qquad (4b)$$

is the actual escapement and $\phi(\cdot,\cdot)$ denotes some suitable functional form. An even more general formulation is possible if the possibility is admitted that the magnitude and timing of the arrivals on the spawning beds are also significant. The loss function must still be expressed in terms of the entire run but the functional form would be of the type

$$L_E(m) = \phi'(E_1, E_2, \ldots E_m; \hat{E}_1, \hat{E}_2, \ldots \hat{E}_m) \qquad (3')$$

where E_i and $\hat{E}_i$ are, respectively, the optimum and actual escapements for the ith time period. However, the determination of the optimum total level of escapement, which is necessary to characterize $\phi(E, \hat{E})$, is a subject of current research and is by no means resolved at present. Thus, the characterization of a function of the generality of $\phi'(E_1, E_2, \ldots E_m; \hat{E}_1, E_2, \ldots \hat{E}_m)$ must await further biological data.

The Bayes risk is defined as the average or expected loss where the averaging is over all possible outcomes and an optimum strategy will be defined as that strategy that minimizes the Bayes risk.[4] An expression for the Bayes risk will now be constructed that is appropriate for the salmon management problem just out-

[3] If the capacity of the cannery becomes limiting, as may happen in cycle years, the loss function for the catch may be written in slightly more general form as

$$L_X(K) = \sum_{i=1}^{k-1} v_i \left\{ \eta_i n_i(\theta) - \min [\hat{\eta}_i n_i(\theta), \mathrm{cap}(i)] \right\} \qquad (2')$$

where cap(i) denotes the cannery capacity for the ith time period. This relation implies that any actual catch that exceeds the cannery capacity will not decrease the corresponding loss. This function is no longer linear but it is still additive. Note also that no cost has been ascribed to the additional economically nonproductive fishing effort. Cannery capacity was one of the constraints imposed by Rothschild and Balsiger in their paper.

[4] The specification of the minimum Bayes risk as the criterion of optimality, while a reasonable one, is somewhat arbitrary. Other criteria are in common use, most notably the "Minimax," in which the optimum strategy is that which minimizes the maximum risk.

lined. Consider the start of the kth time period where $1 \leq k \leq m$ but otherwise arbitrary. The management biologist has at his disposal data observed through the $(k-1)$st period which will be designated by $(\underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1})$. This is an abstract designation for data which may typically be in the form of catch reports, catch per unit effort data, tower counts, etc. By convention $\underset{\sim}{Y}_0$ represents the preseason information, such as the high-seas forecast, that is obtained prior to the start of the run. However, all future outcomes must be considered since the loss function for the escapement is formulated in terms of the final state of the system. The vector $\underset{\sim}{\theta}$, which characterizes both the run and the corresponding set of optimum allocation rules, is, from the biologists' point of view, an unknown parameter whose value he is attempting to infer. Generally $\underset{\sim}{\theta}$ may be considered to have some underlying prior distribution which may be inferred from historical data, etc. As additional data are gathered, the probability density of $\underset{\sim}{\theta}$ may be successively updated to reflect this additional information. Thus the probability density for $\underset{\sim}{\theta}$ at the beginning of the kth period may be written as

$$f_k(\underset{\sim}{\theta} \mid \underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}; \zeta)$$

where the prior data, $(\underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1})$, and the manner in which it is obtained, ζ, appear as conditioning quantities.

Now consider the distribution of the actual allocation $\hat{\eta}_i$. Generally $\hat{\eta}_i$ will be a random variable whose distribution will depend on the action taken, δ_i, and on the true state of nature, $\underset{\sim}{\theta}$. Thus the probability density of $\hat{\eta}_i$ may be written in conditional form as $g_i(\hat{\eta}_i \mid \delta_i, \underset{\sim}{\theta})$. This tacitly assumes that the allocation resulting from a decision taken during any particular time period is independent of the outcomes during any other time period which in turn implies that the individual fish is vulnerable during only a single time period. This condition is generally fairly well satisfied in most of Bristol Bay where the fishing districts are relatively small and the fish do not delay in their upstream migrations. Exceptions occur occasionally during extreme tides when the fish may enter and leave the fishery more than once before proceeding upstream. A similar exception would occur if a fishing district were of sufficient size that individual fish must necessarily spend more than a single time period in it. In these more general cases we must include all prior allocations as conditioning quanitities, i.e., the appropriate density would be of the form $g_i(\hat{\eta}_i \mid \hat{\eta}_1, \hat{\eta}_2, \ldots \hat{\eta}_{i-1}, \delta_i, \underset{\sim}{\theta})$. An equivalent but more concise notation would be to condition the distribution of $\hat{\eta}_i$ by δ_i and by the state of the system at the start of the ith time period, S_i, i.e., $g_i(\hat{\eta}_i \mid \delta_i, S_i)$. That this is an equivalent conditioning follows from our previous definition of the state of the system as reflecting the true state of nature as well as the effects of all previous policy decisions. If we retain the assumption of independence of the allocations, the joint probability density of $(\hat{\eta}_i, \hat{\eta}_2, \ldots \hat{\eta}_m)$ may be written in factored form as

$$g(\hat{\eta}_i, \hat{\eta}_2, \ldots \hat{\eta}_m \mid \delta_1, \delta_2, \ldots \delta_m; \underset{\sim}{\theta}) = \prod_{i=1}^{m} g_i(\hat{\eta}_i \mid \delta_i, \underset{\sim}{\theta}). \tag{5}$$

It is now possible to construct the risk functions appropriate for the start of the kth time period where, as usual, k is arbitrary. The experimental cost, $C(\zeta)$, has been assumed fixed in advance in which case it is equal to its expected value. Thus the first term of the risk, $R_{1,k}(\zeta)$, is given simply by

$$R_{1,k}(\zeta) = C(\zeta) \tag{6}$$

for all k.

The risk function associated with the catch may be thought of as consisting of two parts. The first part is the risk corresponding to the loss already accrued through the kth time period for which the management decisions have already been made. The second is the risk over the remainder of the run for which the decisions $\delta_{k+1}, \delta_{k+2}, \ldots \delta_m$ remain to be made. From (2) and (5) we obtain

$$R_{2,k}(\delta_1, \delta_2, \ldots \delta_k \mid \underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}; \zeta) =$$

$$\sum_{i=1}^{k} v_i \int d\underset{\sim}{\theta}\, f_k(\underset{\sim}{\theta} \mid \underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}; \zeta)$$

$$\int d\hat{\eta}_i\, (\eta_i(\underset{\sim}{\theta}) - \hat{\eta}_i)\, n_i(\underset{\sim}{\theta})\, g_i(\hat{\eta}_i \mid \delta_i, \underset{\sim}{\theta}) \tag{7}$$

for the risk through the kth time period. Although we are considering the start of the kth time period, $\underset{\sim}{Y}_{k-1}$ will have been acquired so that δ_k may be chosen on the basis of this and all previous observations. Similarly, the risk over the remainder of the run is given by

$$R_{3,k}(\delta_{k+1}, \delta_{k+2}, \ldots \delta_m | \underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}; \zeta) =$$

$$\sum_{i=k}^{m} v_i \int d\underset{\sim}{\theta}\, f_k(\underset{\sim}{\theta} | \underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}; \zeta)$$

$$\int d\hat{\eta}_i (\eta_i(\underset{\sim}{\theta}) - \hat{\eta}_i)\, n_i(\underset{\sim}{\theta})\, g_i(\hat{\eta}_i | \delta_i; \underset{\sim}{\theta}) \qquad (8)$$

where, in an implicit sense, the decisions δ_{k+1}, $\delta_{k+2}, \ldots \delta_m$ will be conditional upon the prior decisions $\delta_1, \delta_2, \ldots \delta_k$ as well as upon the observations $\underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}$. Equations (7) and (8) have a similar structure although in Equation (7) we are weighting past decisions by our present knowledge of the state of nature while in Equation (8) the future decisions must necessarily reflect only the information obtained through the (k-1)st time period.

The risk for the escapement is assumed to be nonseparable so that the entire run must be considered at once. The general expression for this portion of the risk is then given by

$$R_{4,k}(\delta_1, \delta_2, \ldots \delta_m | \underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}; \zeta) =$$

$$\int d\underset{\sim}{\theta}\, f_k(\underset{\sim}{\theta} | \underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1}; \zeta) \int d\hat{\eta}_1 \ldots$$

$$\int d\hat{\eta}_m\, \phi[E(\underset{\sim}{\theta}), \hat{E}(\hat{\eta}_1, \hat{\eta}_2, \ldots \hat{\eta}_m)] \prod_{i=1}^{m} g_i(\hat{\eta}_i | \delta_i; \underset{\sim}{\theta}). \qquad (9)$$

The total Bayes risk is then the sum of the risks given by (6), (7), (8), and (9), i.e.,

$$R_k = \sum_{i=1}^{4} R_{i,k}. \qquad (10)$$

These equations have been derived under very general conditions and assumptions with little effort towards characterizing any of the functions indicated. It is interesting to note, however, that loss functions of the same general form as those appearing in the integrands of (7), (8), and (9) may be obtained if we assume 1) a steady state spawner-return relation of the type proposed by Ricker (1958) and 2) the economic loss (or gain) is proportional to the catch. The steady state Ricker spawner-return relation is

$$\hat{N}_{tot} = \theta_1 \hat{E} e^{-\theta_2 \hat{E}} \qquad (11)$$

where the parameter vector $\underset{\sim}{\theta} = (\theta_1, \theta_2)$ describes the run and $\hat{N}_{tot}$ and $\hat{E}$ denote the actual run size and the escapement respectively. The corresponding catch is given by

$$\hat{X} = \theta_1 \hat{E} e^{-\theta_2 \hat{E}} - \hat{E} \qquad (12)$$

from which it follows that the optimum escapement, E, is given by the solution of

$$\frac{d\hat{X}}{d\hat{E}} = 0$$

or

$$\theta_1 (1 - \theta_2 E) e^{-\theta_2 E} = 1. \qquad (13)$$

The appropriate loss function in terms of the catch is

$$L(X, \hat{X}) = \bar{v}(X - \hat{X}) \qquad (14)$$

where $\bar{v}$ is the average unit value of the fish. The equivalent expression

$$L'(E, \hat{E}) = \bar{v}[\theta_1 (E e^{-\theta_2 E} - \hat{E} e^{-\theta_2 \hat{E}}) - (E - \hat{E})] \qquad (15)$$

in terms of the escapement is easily obtained by substituting (12) in (14). The term $\bar{v}\theta_1 [\exp(-\theta_2 E) - \exp(-\theta_2 \hat{E})]$ is nonlinear while $\bar{v}(E - \hat{E})$ is a linear and additive function of the daily escapements. The substitution of (15) into (9) would then result in an integral of the same general form as (9) and two additional integrals corresponding to (7) and (8).

As indicated earlier, the experimental design,

ζ, is usually fixed prior to the start of fishing and, except for minor variations, remains essentially unchanged during the run. We define the optimum experimental design, ζ^*, by

$$\min_{\zeta} R_0(\bar{\delta}_1, \bar{\delta}_2, \ldots \bar{\delta}_m; \zeta) = R_0(\bar{\delta}_1, \bar{\delta}_2, \ldots \bar{\delta}_m; \zeta^*) \tag{16}$$

where the overbars on the $\{\delta_i\}$ denote averaging overall allowable decision rules δ in the set D and the risks are determined prior to the taking of any observations. Similarly, the optimum decision rules $(\delta_1^*, \delta_2^*, \ldots \delta_m^*)$ are that set of decisions that minimizes the average risk over the duration of the run.

DISCUSSION

A mathematical description of a salmon fishery that includes both stochastic and dynamic elements has been formulated although the final result is relatively general and somewhat abstract. Indeed, the mathematics was formulated specifically to simulate the actual assessment and management of the typical Bristol Bay sockeye salmon fishery. The statistician or management biologist periodically acquires additional data, such as catch reports and test fishing results, from which he can make repeatedly more refined estimates of the true state of nature. Also, although perhaps quite unconsciously, he attempts to estimate the losses (or, if an optimist, the gains) associated with any course of action and the relative probability of occurrence of these losses. Then, based on all data obtained to date, including all past decisions and outcomes, he attempts to formulate a future strategy that will minimize his risk. The analysis of the preceding section attempted to express this sequence of events in a more formalized and quantitative manner.

The apparent fidelity of statistical decision theory to the real world suggests that it provides a very general theoretical tool for the description of such processes. However, the implementation of such a theory may give rise to some practical problems of considerable difficulty, some of which were discussed in the Introduction. In particular it was emphasized there that the ability to formulate a problem as a dynamic program or, almost equivalently, as a problem in sequential statistical decision theory, by no means assures that a solution may be obtained. In this section some additional general features of dynamic programming, as they apply to the fisheries management problem just formulated, will be further elaborated.

The set of optimum decision rules has been defined as that set that minimizes the Bayes risk over the duration of the run. From this it follows that the kth decision must be chosen optimally as a function of the set of prior observations $(\underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1})$ and as a function of all prior decisions $(\delta_1, \delta_2, \ldots \delta_{k-1})$. In other words, δ must be chosen at each stage in an optimal manner taking into account all prior observations and decisions. At this point we continue Hillier and Lieberman's (1967) characterization of dynamic programming, the first three principles of which were presented in the Introduction. Their principle number four states that: Given the current state of the system, an optimal policy for the remaining stages is independent of the policies adopted in the previous stages. This is a paraphrase of the fundamental "Principle of Optimality" of Bellman (1957, p. 83) which states that: "An optimal policy has the property that whatever the initial state and initial decision are, the remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision." The principle of optimality thus assures that the policy we have specified is indeed an optimal policy.

The contradiction, which is more apparent than real, will now be resolved between the principle of optimality just stated and our previous contention that the choice of an optimal decision δ_k depends not only on $(\underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1})$ but also on the previous decisions $(\delta_1, \delta_2, \ldots \delta_{k-1})$. Recall that the state of the system at time k, say, S_k, is assumed to be uniquely determined by $(\underset{\sim}{Y}_0, \underset{\sim}{Y}_1, \ldots \underset{\sim}{Y}_{k-1})$, $(\delta_1, \delta_2, \ldots \delta_{k-1})$, and $\underset{\sim}{\theta}$, the true state of nature. The converse is not true, however, since a multiplicity of different decisions and observations may lead to the same S_k, i.e., there is generally no unique path to S_k. Thus, while it is perhaps more appropriate to state that the optimum δ_k is a function only of S_k, it should be borne

in mind that S_k has been uniquely determined by past decisions and observations so that, in an implicit sense, the $\{\delta_i\}(i = 1,...m)$ are not generally mutually independent.

Consider now a typical Bristol Bay salmon fishery. The usual allowable decision rules consist of either opening or closing the fishery. In addition the management biologists also have the option of allowing fishing over an increased or decreased area depending on whether the run is larger or smaller than normal. Thus, in the most general case, a total of four distinct strategies is available although it is unlikely that both increased and decreased fishing areas would be used during a single season.[5] In the usual case, then, a total of three distinct strategies is available each day from which it follows that a total of 3^m separate courses of action may be pursued during a fishing season m days long. Typically m is equal to about 20 days in Bristol Bay so that the total number of allowable strategies is of the order of 10^9. This is not a number to be taken lightly and is an example of what Bellman (1957, p. 6) refers to as "The Curse of Dimensionality."

The principle of optimality, which is particularly useful in multistage allocation processes, may be invoked in an effort to reduce this problem in many dimensions to a sequence of problems in one dimension. Assume that we are at the beginning of the mth time period where the state of the system is characterized by S_m where S_m reflects the observations $(\underset{\sim}{Y}_0, \underset{\sim}{Y}_1,...\underset{\sim}{Y}_{m-1})$ as well as past decisions $(\delta_1, \delta_2,... \delta_{m-1})$. Thus the only decision at our disposal is δ_m and presumably an optimal δ_m may be chosen as a function of S_m. Consider next the beginning of the $(m-1)$st time period for which the system is characterized by S_{m-1}. For every δ_{m-1} selected and executed the system is transformed, after the acquisition of the data $\underset{\sim}{Y}_{m-1}$, into the state S_m for which an optimal decision has already been obtained. Thus at this stage we need optimize only with respect to δ_{m-1}. In this manner we can proceed backward to the beginning of the first time period, characterized by an S_1 depending on Y_0 at which point an optimal δ_1 is selected.

This backward recursive scheme is typical of the method of attack on dynamic programming problems. For a concise but elegant example of this technique applied to a simulated, but numerical, fishery problem see Rothschild (1970). The particular example he used had discrete stages in time with a finite number of strategies available for each stage. The desired solution described the optimum sequence, or path, in time of visiting various fisheries, for a fixed total number of time periods, so that the total catch was maximized. While highly idealized, this problem constitutes a true dynamic program. However, it lacks the stochastic features that are an essential feature of the present discussion.

Verbally this method of solution appears to be most attractive since we have apparently overcome the problem of excessive dimensionality by the recursive consideration of a sequence of problems of lower dimension. This feature is emphasized in the previously cited example presented by Rothschild. However, in problems of larger scale, either in terms of the number of stages or the number of possible states per stage, a rather more subtle problem of dimensionality appears. This concerns the successive specifications of the states of the system $\{S_k\}(k = 1,...m)$. We recall that S_k is characterized not only by $\underset{\sim}{\theta}$, the true state of nature, but all prior observations $(\underset{\sim}{Y}_0, \underset{\sim}{Y}_1,...\underset{\sim}{Y}_{k-1})$ and all prior decisions $(\delta_1, \delta_2,...\delta_{k-1})$. The observation vectors are necessarily multidimensional, each component of which represents a particular piece of data or the observation of a particular entity. To make matters worse, the dimension of the $\underset{\sim}{Y}_i$ will generally increase with i since new forms of data, such as catch reports, tower counts, catch per unit of effort, etc., will become successively available. Thus, the $\{\underset{\sim}{Y}_i\}(i = 0,...k-1)$ required to specify S_k will bring with them their own dimensionality which will soon become overwhelming unless S_k can be described adequately by relatively few parameters. Obviously, aside from possible computer core limitations, the most useful algorithms are those that can accommodate the requisite dimensionality. In a more practical

[5] It is also possible to impose waiting periods for the entry of gear into selected fisheries but this will not be considered here.

sense, however, cognizance must be taken of dimensionality problems to avoid foundering in details, many of which may be irrelevant.

Possible alternative procedures to decrease the number of strategies to consider would be to: 1) combine various contiguous time periods into longer units and thus effectively decrease m and 2) reject those strategies that, based on the value of Y_0 available, have a sufficiently high a priori probability of being nonoptimal. The combining of time periods would be particularly appropriate near the beginning and end of the run when relatively few fish are entering the fishery and the consequences of nonoptional procedures are not so serious. Also, the necessity to consider increased or decreased fishing areas can often be resolved prior to the start of fishing by consideration of the preseason information contained in $\underset{\sim}{Y}_0$.

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THE LIFE HISTORY AND TROPHIC RELATIONSHIP OF THE NINESPINE STICKLEBACK, *PUNGITIUS PUNGITIUS*, IN THE APOSTLE ISLANDS AREA OF LAKE SUPERIOR[1]

BERNARD L. GRISWOLD[2] AND LLOYD L. SMITH, JR.[3]

ABSTRACT

The ninespine stickleback is an important food of juvenile lake trout in the Apostle Islands area. It is the most numerous fish of the area and is distributed in deep waters during the winter and in shallow waters during the summer. Females grow faster than males, reaching an average total length of 80 mm at age 5. Males live to age 3 and attain an average length of 66 mm. Annulus formation on otoliths is complete by mid-July. Seasonal growth is more than half complete by early August; growth of mature females is delayed until after spawning.

Both sexes mature over a period of 3 yr. Spawning occurs from mid-June to late July. Males apparently do not live as long as females, possibly because of a post-spawning mortality. Egg number is a linear function of fish length, although this relationship is different for fish from two separate areas. Environmental differences between these areas, which may affect spawning time, possibly cause the differences in fecundity. Significant quantities of maturing eggs atrophy just prior to spawning, a phenomenon which changes the fecundity relationship.

Sticklebacks eat a variety of invertebrates, particularly the crustaceans *Mysis relicta* and *Pontoporeia affinis*. Food eaten by the stickleback and slimy sculpin is similar, but the adaptability of both species tends to eliminate serious competition. The lake trout is the only serious predator of stickleback.

Investigations were made by the Bureau of Commercial Fisheries (BCF) on the biology of the fishes of Lake Superior from the early 1960's. These studies have been primarily life history studies on economically valuable species such as the lake trout, *Salvelinus namaycush* (Walbaum), various coregonids, and the smelt, *Osmerus mordax* (Mitchill). Some of the more comprehensive of these include Bailey (1964), Dryer (1963), and Dryer and Beil (1964).

When it became apparent that these fish stocks were being rapidly modified by exotic species, particularly the sea lamprey, *Petromyzon marinus* L., additional emphasis was placed on ecological studies of noncommercial fishes whose life histories are interrelated with the exploited ones. One of these, the ninespine stickleback, occurs in BCF index trawl samples in greater numbers than any other. However, prior to the study presented in this paper, its ecological significance in these waters was largely unknown. This study was designed to investigate the life history of the ninespine stickleback in the Apostle Islands region of Lake Superior and determine the importance of its relationships to the economically important fish species of the area.

The ninespine stickleback is one of the most widely distributed northern fishes, occurring in freshwater, estuarine, and coastal saltwater environments (Bigelow and Schroeder, 1953). It is abundant in cool-water habitats similar to Lake Superior throughout the Northern Hemisphere. In middle western United States, it is found in all the Great Lakes except Lake Erie

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(Hubbs and Lagler, 1958). It has also been taken in inland lakes as far south as northern Indiana (Nelson, 1968a), and Moore and Braem (1965) found small numbers in some Lake Superior tributaries. It is a fish of cool, quiet water (Hubbs and Lagler, 1958), and it is generally abundant wherever it occurs in lakes or seas within its range.

METHODS AND MATERIALS

The data for the present study were collected in 1967-69 in cooperation with the BCF Great Lakes Biological Laboratory, Ann Arbor, Mich.[4]

Experimental sampling operations were conducted aboard the BCF research vessel *Siscowet* in conjunction with sampling by BCF in the Apostle Islands, Lake Superior. The main objectives of the BCF program were to enumerate juvenile lake trout, monitor spawning success, measure the impact of the lamprey on the trout population, and contribute research on the biology of other species in the lake.

One of the main objectives of the ninespine stickleback study was to define ecological relationships between the stickleback and other fish, particularly the lake trout. With this objective in mind, and within the limitations of the ongoing BCF program, sampling was essentially confined to seven stations within the Apostle Islands (Figure 1). Five of these stations (12, 24, 44, 75, and 86) were sampled regularly as juvenile trout index trawl stations and yielded data pertinent to questions of species interaction. Comparatively, they supported varying numbers of trout and sticklebacks, and historically they comprised the known lake trout nursery areas within the islands. At present, only stations 75 and 86 support good populations of juvenile trout. The other two stations, 2 and 3, support abundant midsummer stickleback populations and comprise shallow, inshore areas. These two stations were outside the regular BCF trout index sampling routine and required special sampling. Collections from these stations provided data for stickleback age and growth studies and supportive information about distribution and relative abundance.

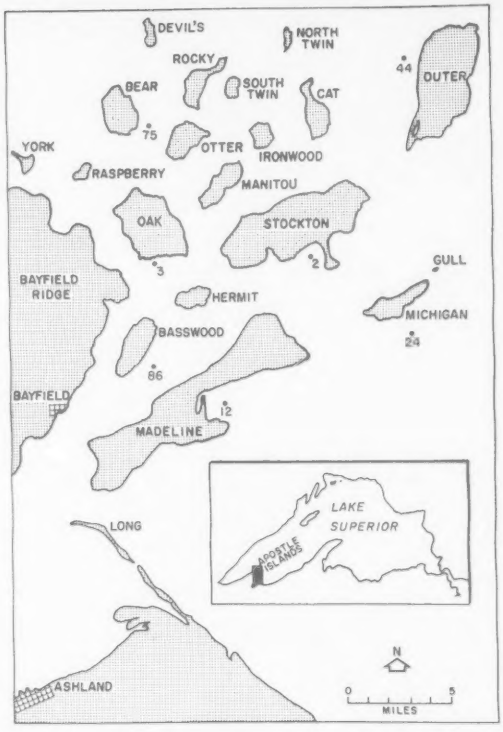

FIGURE 1.—Sampling stations in the Apostle Islands. Blacked out area in inset shows location of these islands in Lake Superior.

A small semi-balloon otter trawl with a 4.7-m headrope, 38.1-mm mesh body (stretched measure), and 12.7-mm mesh cod end was used from a 16-ft aluminum boat with a 40-horsepower outboard motor at stations 2 and 3. A large trawl of the same type (9.4-m headrope, 50.8-mm body, and 12.7-mm cod end) was used aboard the *Siscowet* for deepwater trawling. Adult lake trout were sampled with experimental gill nets ranging from 1.3- to 7.6-cm mesh (bar measure). Zooplankters and sticklebacks examined for stomach contents were collected with a sled-borne plankton net with a 1-m square mouth and 0.158-mm mesh, the bottom edge of which ran approximately 30 cm above the lake bottom. Temperature profiles

[4] Presently the Great Lakes Fishery Laboratory, U.S. Bureau of Sport Fisheries and Wildlife.

were obtained by bathythermograph at each station.

Trout index trawling aboard *Siscowet* was done for two 2-wk periods annually, one spring and one fall. A total of 286 tows, each 1 mile long, were conducted during the stickleback study from April 1967 through May 1970. Additional records from 322 index tows taken in all ice-free months dating back to April 1965 were also included in the study of distribution. A total of 46 ¼-mile tows were made from June through September, 1968 and 1969, with the small outboard trawl, and 18 tows were made with the sled at various times of the year at the index stations in 1968 and 1969. Trawl samples were separated by species, and the fish were counted. After lake trout were measured, fish samples were put in jars of appropriate size and preserved in 10% Formalin.[5] Samples from the plankton sled were flushed directly into jars and preserved in Formalin.

The main limitation of this sampling scheme was that the index trawl series was conducted at a limited number of stations representing trout nursery areas. It is possible that the biological communities and the resultant ecological interrelationships in these areas may not be representative of the entire Apostle Islands area. Also, since areas of sampling were limited and the efficiency of the index trawl was unknown, it was impossible to estimate absolute biomass of the stickleback population. Alternate methods of population estimation were unfeasible because of the immensity of the population and the area.

Additional methods are discussed in appropriate sections throughout the paper.

DESCRIPTION OF GROWTH

Sticklebacks used for age and growth studies were stratified by length, subsampled if catches were large, and frozen. Otoliths (sagittae) were removed, cleaned, dried in alcohol, cleared in creosote, and mounted on microscope slides in Canada balsam as described by Jones and Hynes (1950). The otoliths contained a series of transparent and opaque rings, and it was evident that the transparent zone was laid down at the beginning of the growing season in late June and early July. Therefore, the annulus was considered the outer edge of the opaque zone. Nomographs, based on the male and female body length-otolith length curves, respectively, were used to calculate body length at each annulus (Carlander and Smith, 1944).

Validation of the Otolith Method

Determination of age from otolith rings was made with little difficulty. In older fish the annulus on the outer margin was not as distinct as in young fish, but usually could be identified at the posterior portion of the otolith. After two independent age determinations of 808 pairs of otoliths, 37 pairs required reexamination because the first two were not in agreement.

Otoliths were analyzed from sticklebacks taken with experimental trawls in 1967 and 1968. The samples represented six year classes and five age-groups. The otoliths were from 372 fish taken at station 2 and 436 taken from station 3. Length-frequency distributions were estimated from 18,175 fish measured from 80 trawl samples.

The following evidence indicates that annuli on otoliths provide an accurate measure of stickleback age and growth:

1. Length distribution by age-group based on otolith readings and modes in length-frequency distribution of all measured fish were in close agreement; however, most distributions exhibited some degree of overlap (Figure 2 and 3). In the June sample (Figure 2), the distribution of age-group 0 fish truncated on the left-hand side because it had been discovered that all of these smaller fish were of 0-group.
2. Calculated lengths at the end of each year of life corresponded well between the various year classes (Tables 1 and 2).
3. There was a general increase in average body length with assigned age of the fish (Tables 3 and 4).
4. The average empirical length of aged fish collected in spring prior to annulus for-

[5] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

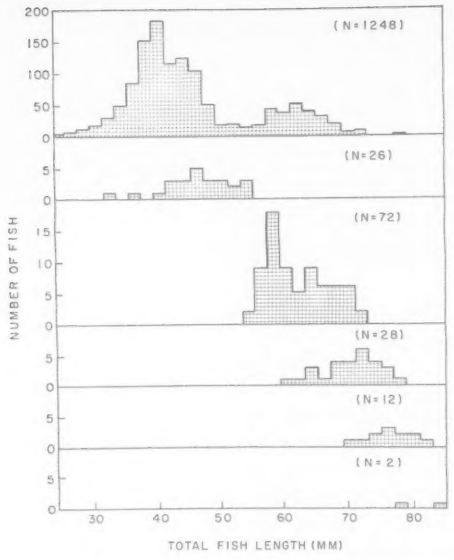

FIGURE 2.—Length-frequency distribution of sticklebacks (top graph) and length frequencies of age-groups 0 to IV based on otolith readings (lower graphs) of fish collected in June 1967. *N* equals number of fish.

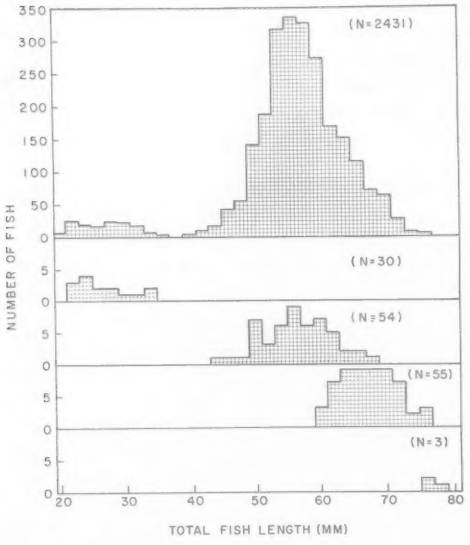

FIGURE 3.—Length-frequency distribution of sticklebacks (top graph) and length frequencies of age-groups 0 to III based on otolith readings (lower graphs) of fish collected in August 1967. *N* equals number of fish.

TABLE 1.—Average calculated total lengths in millimeters of female ninespine sticklebacks from stations 2 and 3 in the Apostle Islands.

Station	Year class	Number of fish	Years of life 1	2	3	4	5
3	1962	1	45.50	58.75	65.75	74.00	81.00
2	1963	16	46.25	58.25	66.25	73.50	
3	1963	19	48.75	61.53	68.56	76.62	79.00
2	1964	24	44.90	61.20	69.16		
3	1964	40	47.38	61.64	68.79	74.92	
2	1965	60	48.65	61.81	70.50		
3	1965	122	48.66	63.25	70.66		
2	1966	110	47.33	63.22			
3	1966	70	48.47	61.18			
2	1967	24	49.00				
3	1967	2	47.75				
[1]2		234	234	88	23	8	
[1]3		254	254	62	38	9	2
[2]2			47.22	61.87	68.63	73.50	
[2]3			47.75	61.27	68.44	75.18	80.00
Average empirical length of fish in spring prior to annulus formation			47.08	62.32	71.16	77.53	81.00

[1] Total number of fish.
[2] Grand average calculated length.

TABLE 2.—Average calculated total lengths in millimeters of male ninespine sticklebacks from stations 2 and 3 in the Apostle Islands.

Station	Year class	Number of fish	Years of life 1	2	3
3	1963	8	45.21	60.23	66.13
2	1964	8	44.25	59.25	65.50
3	1964	38	43.97	59.73	
2	1965	12	44.25	59.62	
3	1965	70	47.30	60.47	
2	1966	108	49.72	62.70	
3	1966	44	48.54	59.70	
2	1967	10	50.60		
3	1967	22	47.00		
[1]2		138	138	38	8
[1]3		182	182	50	2
[2]2			47.20	60.52	65.50
[2]3			46.40	60.03	66.13
Average empirical length of fish in spring prior to annulus formation			48.55	60.60	67.60

[1] Total number of fish.
[2] Grand average calculated length.

mation agreed closely with grand average back-calculated length of each assigned age-group (Tables 1 and 2). Empirical lengths slightly exceeded calculated lengths, indicating seasonal growth may already have begun.

TABLE 3.—Length frequency of the age-groups of female sticklebacks taken in July 1968 from the Apostle Islands.

Total length (mm)	Age-groups				
	I	II	III	IV	V
40-41	5	—	—	—	—
42-43	4	—	—	—	—
44-45	8	—	—	—	—
46-47	10	—	—	—	—
48-49	9	—	—	—	—
50-51	18	—	—	—	—
52-53	6	—	—	—	—
54-55	8	3	—	—	—
56-57	10	9	—	—	—
58-59	7	20	—	—	—
60-61	7	14	—	—	—
62-63	4	13	—	—	—
64-65	4	17	2	—	—
66-67	1	10	1	—	—
68-69	1	17	6	—	—
70-71	—	28	12	1	—
72-73	—	16	16	—	—
74-75	—	6	15	3	—
76-77	—	3	10	2	1
78-79	—	—	7	4	—
80-81	—	1	1	—	2
82-83	—	—	—	1	—
84-85	—	—	—	—	—
86-87	—	—	—	1	—
Average length	52.3	66.5	73.8	76.8	78.5
Number of fish	102	157	70	12	3

TABLE 4.—Length frequency of the age-groups of male sticklebacks taken in July 1968 from the Apostle Islands.

Total length (mm)	Age-groups		
	I	II	III
46-47	5	—	—
48-49	1	—	—
50-51	4	—	—
52-53	2	—	—
54-55	11	—	—
56-57	12	—	—
58-59	11	—	—
60-61	7	5	—
62-63	13	5	—
64-65	7	8	1
66-67	4	18	—
68-69	1	8	1
70-71	—	4	4
72-73	—	2	1
74-75	—	4	2
Average length	51.8	66.7	69.4
Number of fish	78	54	9

Growth in Length

The relationship between total fish length and otolith length was estimated from otoliths of 320 males and 488 females. Body lengths at each 1.0-mm interval of otolith length were averaged, and the mean total lengths were plotted against the otolith length. The relationships for fish from stations 2 and 3 were very nearly the same, but the relationship for males and females were empirically quite different (Figure 4). Second degree polynomial regressions were fitted to these data and the resulting equations were:

$$\text{Males} \quad Y = -25.864 + 2.146X - 0.011X^2$$
$$\text{Females} \quad Y = -25.075 + 2.131X - 0.0010X^2$$

where Y = total fish length (mm) and
X = projected anterior otolith radius (mm).

Coefficients of determination (r^2) values were 0.978 and 0.958 for male and female equations, respectively. An analysis of covariance showed the elevation was significantly different at the 0.01 level ($F_{1,78} = 48.32$). Therefore, growth parameters were calculated separately for each sex. In Figure 4, the plots were extrapolated to intercept the body-length axis at 6 mm, the length of otolith formation of Alaskan threespine sticklebacks (Jones and Hynes, 1950).

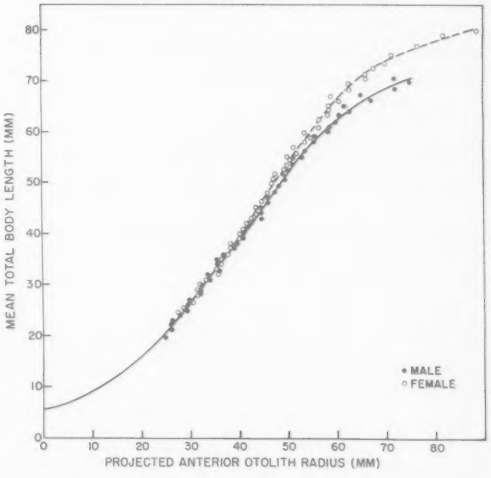

FIGURE 4.—Body length-otolith length relationship for Apostle Islands ninespine sticklebacks. Solid line, males; dashed line, females.

Growth rates were determined for females for the 1962 through 1967 year classes (Table

1) and for males for the 1963 through 1967 year classes (Table 2). Females averaged 47.5, 61.6, 68.5, 74.3, and 80.0 mm in total length at the first through fifth annuli, respectively. Age-groups I, II, and III in males averaged 46.7, 60.2, and 65.6 mm. There was little difference between growth rates of fish from stations 2 and 3. Females from station 2 were longer at the end of 2 of 5 yr of life, and males from station 2 were longer at the end of 2 of 3 yr of life. Females grew faster than males during the first year, being 0.02 and 1.35 mm longer at stations 2 and 3, respectively, at annulus I. These differences increased to almost 3 mm after 3 yr. Females reached age 5, males age 3.

Both sexes showed the greatest growth in length in their first year (Tables 5 and 6), when females attained about 60% and males about 70% of maximum size. The average annual increment calculated from the summation of annual increments was about 30% for both sexes during the second year and on the order of 10% per annum thereafter.

Annulus formation was evident in some sticklebacks as early as June in 1967, and all annulus formation was complete by the second week in July. Annulus formation occurred before spawning and started when surface water temperatures reached about 10°C in 1967 and 1968.

Percentage of annual growth completed at any date during the growing season was computed by comparing the length at capture on a given date in 1967, an average growth year as indicated by average annual increments, with the calculated length at annulus formation in 1968 (Table 7). Male growth was faster at the beginning of the growing season with about 50% of the annual growth being completed by late July. Early seasonal growth of females was slower than in males, and 50% of the annual growth was not complete until mid-August. Growth then declined and was complete or nearly complete in all fish by early December when fall turnover occurred. These calculations are consistent with length-frequency distributions of fish from stations 2 and 3 (Figures 5 and 6). These monthly distributions show that growth, as indicated by increasing modal length of the two apparent age-classes, had begun by July and continued into December.

Older fish had a tendency to grow slower in their first years of life than the younger fish (Tables 1 and 2). This growth pattern (Lee's phenomenon) has been reported for many fish

TABLE 5.—Grand average increment in total length of female ninespine sticklebacks from stations 2 and 3 expressed in millimeters.

Station	Year of life	1962	1963	1964	1965	1966	1967	Mean	Sums of means	Percentage of increment
2	1	—	46.25	44.90	48.65	47.33	49.00	47.22	47.22	—
3	1	45.50	48.75	47.38	48.66	48.47	47.75	47.75	47.75	—
2	2	—	—	12.00	16.30	13.16	15.89	14.33	61.55	30.3
3	2	—	13.25	12.78	14.26	14.59	12.71	13.51	61.26	28.2
2	3	—	—	—	8.00	7.96	8.69	8.21	69.76	13.3
3	3	—	—	7.00	7.03	7.15	7.41	7.14	68.40	11.6
2	4	—	—	—	—	7.25	—	7.25	77.01	10.3
3	4	—	—	—	8.25	8.06	6.13	7.48	75.88	10.9
3	5	—	—	—	—	7.00	2.38	4.69	80.57	6.1

TABLE 6.—Grand average increment in total length of male ninespine sticklebacks from stations 2 and 3 expressed in millimeters.

Station	Year of life	1963	1964	1965	1966	1967	Mean	Sums of means	Percentage of increment
2	1	—	44.25	44.25	49.72	50.60	47.20	47.20	—
3	1	45.21	43.97	47.30	48.54	47.00	46.40	46.40	—
2	2	—	—	15.00	15.37	12.98	14.45	61.65	30.6
3	2	—	15.02	15.76	13.17	11.18	13.78	60.18	29.6
2	3	—	—	—	6.25	—	6.25	67.90	10.1
3	3	—	—	5.90	—	—	5.90	66.08	9.8

TABLE 7.—Percent growth completed at various dates of the 1967 season for ninespine sticklebacks in the Apostle Islands.

Date	Male			Female				
	0	I	II	0	I	II	III	IV
July 22-27		48	75		28	5	37	75
August 8-19	62	69	98	64	54	27	60	
December 4	100	100	100	100	97	79	85	100

species (Lee, 1912). In the Lake Superior study, there appeared to be no significant disappearance of faster growing individuals from the length-frequency distributions (Figures 5 and 6). However, as will be shown below, there does appear to be a sex-specific mortality associated with spawning. Since faster growing males tend to spawn at an earlier age, slower growing males may be left in the population

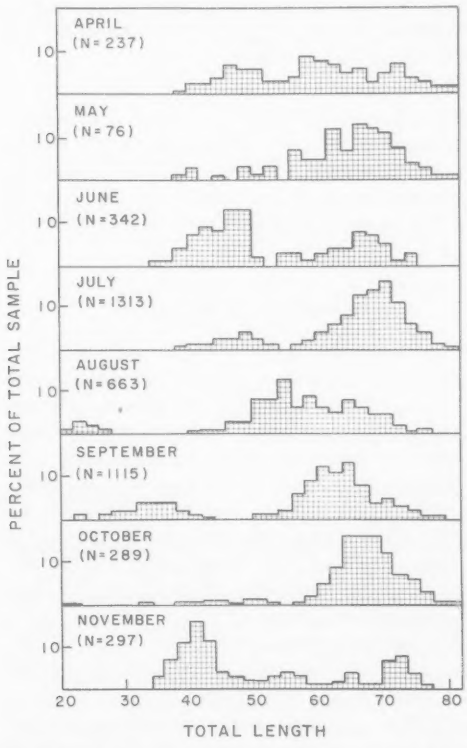

FIGURE 5.—Length-frequency histograms of station 2 sticklebacks expressed in millimeters. *N* equals number of fish in sample.

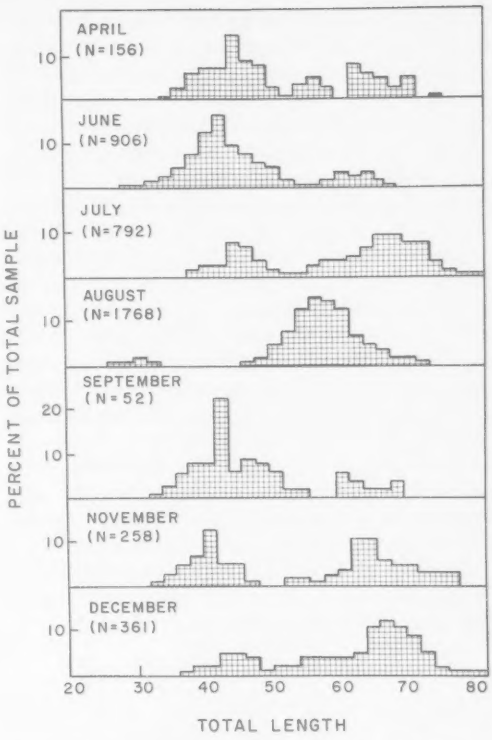

FIGURE 6.—Length-frequency histograms of station 3 sticklebacks expressed in millimeters. *N* equals number of fish in sample.

longer. This tendency does not explain the presence of "Lee's phenomenon" among females, where it is most prevalent. Figures 5 and 6 demonstrate that young-of-the-year fish were being sampled throughout the latter part of each season. Therefore, it is possible that biased sampling of precocious individuals in the younger age-groups creates the appearance that younger fish of both sexes are growing more rapidly than older fish did at the same age. To minimize these suspected biases in the growth-rate calculations, back calculations for each year class over successive collection years were averaged as unweighted means.

Growth was fairly stable from year to year (Tables 5 and 6) with the exception of 1964. No explanation for this poor growth year was discovered.

Ninespine sticklebacks from Lake Superior grow as large, or larger, than those reported in other areas. The most comprehensive growth calculations on the ninespine stickleback prior to this study was done by Jones and Hynes (1950) on a population in a small English stream. They found fish reached only 37 mm in 1 yr and 46 mm in 3 yr. The largest fish recorded was 55 mm. These fish were in direct competition with a population of threespine sticklebacks. Nelson (1968b) found the largest fish in a northern Indiana lake to be 67.3 mm. Bertin (1925) and Leiner (1934) both record European ninespine sticklebacks over 80 mm, but Blegvad (1917) found none over 50 mm in Danish brackish waters. McKenzie and Keenleyside (1970) report fish up to 75 mm in Lake Huron. The formula, TL = 1.14SL, was calculated from 300 Lake Superior fish and used to convert reported SL (standard length) to TL (total length) for these comparisons.

Walford (1946) proposed a transformation of growth data to be expressed as a straight line described by the equation:

$$L_{t+1} = L_\infty (1\text{-}K) + KL_t,$$

where L_{t+1} = body length at age $t+1$
L_t = body length at age t
L_∞ = ultimate length
K = slope.

The ultimate length is found graphically where the Walford line intersects a line drawn at 45° through the origin of the graph and is theoretically the greatest length a fish of the population will attain. The slope of the line, K, indicates the decrease in growth rate.

Walford lines were plotted for Apostle Islands sticklebacks from stations 2 and 3 (Figure 7). Means of stations 2 and 3 grand average calculated lengths at each annulus were used to combine station data for each sex.

Calculated values were:

Males	K	=	0.411
	L_∞	=	69.690
Females	K	=	0.672
	L_∞	=	87.660

The ultimate length for males is less than expected from what is known about male length frequency (Table 4). This is probably due to the small number of points used because of the short life span. More points can be included for the female relationship, and the ultimate length is reasonable.

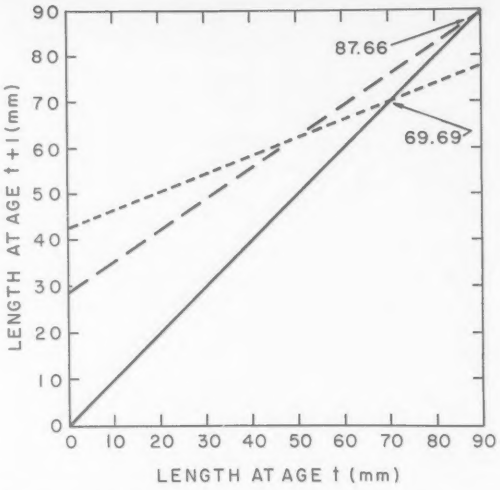

FIGURE 7.—Walford lines for Apostle Islands ninespine sticklebacks. Short dashed line, males; long dashed line, females.

Growth in Weight

Plots of weight against length were made for males and females by calculating average weights for fish at 1-mm intervals. Weights for females in the mature size range were less than male weights. The cause for this was the abrupt drop in weight of females which had just spawned, since the mature female gonad accounts for up to 10% of total fish weight. After females collected in late June and July were omitted from the length-weight plots, the lines for males and females appeared similar.

Analysis of covariance showed slope, and intercept differences were nonsignificant at the 0.05 level ($F_{1,745} = 2.71$ and $F_{1,746} = 1.36$, respectively), and the data were pooled to calculate a length-weight relationship. The resultant regression included 748 fish and was described by the formula:

$$\log W = -4.5681 + 3.2190 \log L$$

where $\log W$ = common log of the weight (0.1g)
and $\log L$ = common log of the length (mm).

Growth in weight was calculated on the basis of weight at the time of each annulus formation (Table 8). The greatest increment in weight occurred in the second year of life for both sexes at both stations. After the second year, growth in weight declined rapidly, but the decline was more pronounced in males.

Instantaneous rates of growth in weight between consecutive ages varied from 0.804 to 0.223 for males and from 0.842 to 0.192 for females.

TABLE 8.—Calculated weight attained by Apostle Islands sticklebacks at the time of annulus formation.

	Male			Female		
Age-group	Total length (mm)	Calculated weight (g)	Percentage increment	Total length (mm)	Calculated weight (g)	Percentage increment
Station 2						
I	47.20	0.662	—	47.22	0.663	—
II	60.52	1.470	122.0	61.87	1.580	138.3
III	65.50	1.821	23.9	68.63	2.215	40.2
IV	—	—	—	73.50	2.751	24.2
Station 3						
I	46.60	0.627	—	47.75	0.687	—
II	60.03	1.401	123.4	61.27	1.494	117.4
III	66.13	1.955	39.5	68.44	2.185	46.2
IV	—	—	—	75.18	2.955	35.2
V	—	—	—	80.00	3.624	22.6

DISTRIBUTION

While some species of sticklebacks can be found in a marine environment far from shore, the ninespine stickleback is an inshore species (Bigelow and Schroeder, 1953). Hubbs and Lagler (1958) state that the species is abundant in the Isle Royale and Keewenaw Bay areas of Lake Superior. BCF operations found sticklebacks in Nipigon Bay, on the north shore of the lake. While sticklebacks were found throughout the Apostle Islands, it should not be concluded that these fish are similarly abundant on all Lake Superior shorelines. Anderson (1969) recovered only 0.1 stickleback per trawl tow in 90 tows in the Duluth area, sampling during all ice-free months. Degradation of water quality may well be the explanation for this; however, no historical records of stickleback abundance in the Duluth area are available to help justify this hypothesis.

Temperature profiles were secured concurrently with trawl tows. Sticklebacks were found in the warmer deep water in early spring, but were evenly distributed at all depths during spring turnover (Table 9). In midsummer they congregated on the warm shallow snoals where water temperatures reached as high as 20°C. When the fall turnover occurred in September, they were again fairly evenly distributed at all depths. By November the fish were beginning to congregate in the deeper water and were found there in great numbers during December. No data are available for midwinter, but it is assumed the deepwater habitat is used at this time since they were abundant there the following spring. Nelson (1968b) also noted sum-

TABLE 9.—Average numbers of sticklebacks caught per 30-min trawl tow each month at various depths during 1967-69.

[Numbers of tows are in parentheses.]

Depth (fathoms)	Apr.	May	June	July	Aug.	Sept.	Nov.	Dec.
3-9	0.0 (2)	2.7 (4)	12.8 (6)	615.7 (16)	641.5 (12)	75.4 (5)	0.3 (5)	
10-26	0.3 (15)	8.4 (11)	14.8 (45)	10.5 (17)	11.4 (16)	80.0 (42)	18.2 (15)	
27-50	58.4 (12)	11.7 (3)	32.7 (16)	0.1 (6)	0.0 (1)	147.1 (9)	114.7 (11)	267.3 (4)

mer inshore migrations of ninespine sticklebacks in Crooked Lake, Ind.

The shoal areas where sticklebacks concentrated in the summer were represented by stations 2 and 3 (Figure 1). Station 2 included a sandy beach, approximately 2 miles long, at Presque Isle Bay, Stockton Island, which gradually deepened and merged with the soft bottom muds of the deeper areas. In summer sticklebacks congregated in large numbers on the beach in ½ to 2 fathoms of water. The fish could easily be seen by eye and were evenly distributed over the bottom throughout the entire beach area. Station 3, along the south shore of Oak Island, was characterized by a sandy shelf about ¼ mile wide paralleling the shore which gradually deepened to 8 fathoms. The bottom then dropped steeply to 12 fathoms. This steep slope was covered with a dense growth of *Nitella* sp. The summer concentration of sticklebacks occurred in this vegetation. No fish could be seen over the sandy shelf, and no fish were caught unless the net was recovered with mats of *Nitella* sp. clinging to it.

Dryer (1966), Anderson and Smith (1971), and field observations by the senior author of this paper indicate that smelt, slimy sculpins, lake trout under 28-cm TL, and trout-perch, *Percopsis omiscomaycus* (Walbaum), had food habits similar to the stickleback and were apparently abundant enough to be potential competitors with the stickleback. Rank correlation coefficients (r_s) were obtained between the average number of sticklebacks caught per 1-mile trawl tow (CPE) and the CPE of these potential competitors in 100 trout index tows. The CPE's were ranked for each species, ties being given the mean rank, and r_s values were determined by the formula presented by Snedecor (1956). The 100 tows were randomly selected from all (322) trout index tows made at stations 86, 75, 44, 24, and 12 from 1965 to 1968. The significant relationships were those for juvenile smelt, trout-perch, and slimy sculpins (Table 10). Sticklebacks inhabited different areas than juvenile smelt and trout-perch, and sticklebacks and sculpins inhabited the same areas, at least during spring and fall. The results of the correlations do not preclude significant relationships at other times of the year or other places, nor do they consider possible effects of differences in availability to the gear. Further discussion of these correlations will be presented in the section on food habits.

TABLE 10.—Rank correlation coefficients (r_S) between stickleback CPE and CPE's of other species in 100 randomly selected index trawl tows in the Apostle Islands, 1965-68.

Species	r_S
Juvenile lake trout to 11 inches	−0.077
Smelt adults	+0.073
Smelt juveniles	−0.461**
Slimy sculpin	+0.568**
Trout-perch	−0.360**

**Significant at 0.01 level (98 degrees of freedom).

RELATIVE ABUNDANCE

Dryer (1966) reported that the ninespine stickleback was the most abundant species in 578 Apostle Islands experimental trawl tows from 1958 through 1963. The average CPE of stickleback during this period was 51.8. Smelt ranked second (CPE = 40.4), and slimy sculpin, *Cottus cognatus* Richardson, were third (CPE = 22.3). Lake trout CPE was 6.8.

Over the 1965-68 period, 322 trout index tows were made, and the relative rank of sticklebacks, smelt, and slimy sculpins was unchanged from the 1958-63 period (Table 11). The CPE's were 61.1, 50.3, and 17.7, respectively. The catch statistics of the two time periods show slight increases for sticklebacks, smelt, and lake trout. Further comparison is meaningless however, because sampling allocations between index stations used in the two time periods were not identical, and extreme between-tow variation was observed. Table 11 does not include data from stations 2 and 3 because they were not used by BCF as trout index trawl stations.

To sample the shallow inshore area of station 2, where sticklebacks congregated in midsummer, ¼ mile tows were made with the small outboard trawl. The wingspread opening of the trawl was determined by measuring the width of the trawl path on the bottom as indicated by ground-rope disturbance immediately after the

TABLE 11.—Average catch per 1-mile trawl tow (CPE) at various index stations in the Apostle Islands calculated from Bureau of Commercial Fisheries index trawling data, 1965 through 1968.

Species[1]	Station					Weighted mean
	86	75	24	12	44	
Number of tows	99	98	28	76	21	
Stickleback	42.13	93.22	53.52	60.01	4.69	61.11
Smelt	88.44	19.87	20.71	52.33	7.90	50.30
Lake trout	23.16	7.63	4.29	4.63	.76	10.71
Slimy sculpin	7.93	19.63	38.43	20.01	18.57	17.71
Fourhorn sculpin	.38	.72	.36	4.20	1.14	2.00
Spoonhead sculpin	.35	.47	.61	3.29	.14	1.06
Mottled sculpin	.04	.01	—	—	—	.01
Lake whitefish	.76	1.06	.14	.12	3.62	.81
Bloater	4.44	5.38	—	7.30	.33	4.63
Shortjaw cisco	.08	.06	—	.18	—	.08
Kiyi	.01	.01	—	—	—	<.01
Lake herring	.12	.05	—	.14	—	.08
Unidentified coregonid	5.80	.56	—	1.37	1.24	2.30
Round whitefish	1.00	—	13.93	—	13.33	2.03
Pygmy whitefish	.28	.71	.25	1.24	.86	.65
Alewife	.01	.04	—	—	—	.01
Trout-perch	3.08	1.02	.11	.17	7.28	1.69
Burbot	.17	1.03	.43	.45	.10	.50
Longnose sucker	.07	.14	—	—	—	.06
Johnny darter	.01	—	—	—	—	<.01

[1] Taken from: Bailey, R. M. (chairman). 1970. A list of common and scientific names of fishes from the United States and Canada. Am. Fish. Soc., Spec. Publ. 6, 149 p.

trawl was towed through the area. This allowed estimation of minimum density.

Catches with this trawl were highly variable even though visual sightings, during both day and night, indicated fish were quite evenly distributed. Light obviously influenced catch because no fish were caught during the daylight hours even though they could be seen. Moonlight intensity probably influenced the catch, as did wind direction and intensity, by adversely affecting the efficiency of the sampling operation. It is entirely possible these factors also influenced catches by *Siscowet* in deeper waters.

Summer nighttime trawl tows on the sandy beach, station 2, usually caught from 300 to 2,500 sticklebacks in ¼ mile (Table 12). These values correspond to minimum density estimates of 0.18 to 1.49 fish per square meter. Sticklebacks were the only species caught in the area during their summer concentration, but johnny darters, *Etheostoma nigrum* Rafinesque, pygmy whitefish, *Prosopium coulteri* (Eigenmann and Eigenmann), trout-perch, and smelt were found there in spring and fall.

TABLE 12.—Catches of sticklebacks in 1967 and 1968 on the sand beach of station 2 during the night using the 4.7-m otter trawl and outboard.

Month	Number of tows	Total sticklebacks	Average per tow
April	5	6	1.2
June	3	217	72.3
July	10	6,985	698.5
August	8	7,564	945.5
September	4	3,622	905.4
November	4	0	0.0

REPRODUCTION

Maturation

The gonads of 401 spring-collected fish from which otoliths were extracted were analyzed for maturity. In addition, 34 male and 72 female I annulus fish (determined from length-frequency histograms) were included in maturity studies.

Both male and female sticklebacks matured over 3 yr (Table 13). A greater percentage of males matured at age 1, with large size being a prerequisite for early maturity. By age 2, nearly all fish of each sex were sexually mature, but neither sex was 100% mature until the third year of life. Jones and Hynes (1950) found 99% of a sample of European ninespine sticklebacks mature with 2 yr.

TABLE 13.—Percent of Apostle Islands sticklebacks mature at each annulus with total number of fish in each group in parentheses.

	I's under 50 mm	I's 50 mm and over	II	III	IV	V
Male	34 (56)	56 (40)	93 (78)	100 (10)		
Female	5 (89)	35 (67)	97 (106)	100 (44)	100 (15)	100 (2)

Within the ovaries, several developmental groups of ova can be distinguished. The ovaries were classified into the following stages for maturity:

Immature (I)

Preserved in Formalin, the ova was translucent, spherical, and invisible to the naked eye. Ova of this group are present in the ovaries throughout the year. Ovaries in this stage are slender, elongate, white organs.

Intermediate (II)

The first yolk granules appear in this stage giving the ovary a pale yellowish tinge while making the ova visible without magnification.

Maturing (III)

The yolk granules appear as highly refractive, spherical bodies in the cytoplasm, and ova become opaque. The ovary becomes turgid and deep yellow in color, with ova readily visible but firmly embedded in the follicles. The size of ova in this stage varies widely.

Ripe (IV)

When the ova are about ready to be spawned, a single conspicuous golden oil globule appears in the yolk. The ova readily break from the follicles in which they were formed and flow freely from the oviduct when the sides of the fish are pressed. In Formalin-preserved fish, mature ova can readily be separated from ovarian tissue with a dissecting needle, a procedure which was almost impossible in Stage III fish. The fish is very rotund.

Partly spent (V)

Partly spent fish contained ripe ova but not the full complement. The ova are congregated in the anterior ends of the ovaries, with the posterior portion somewhat flaccid and lighter in color.

Spent (VI)

Ovaries were gradually resuming the appearance of those in the intermediate stage. Ova maturing for the next reproductive period are already visible to the naked eye. Following spawning, resorbing ova remnants were sometimes found.

Female fish were judged to be sexually mature when their ovaries contained ova in developmental Stage II or beyond. Male maturity was established by noting the presence of breeding color, an ink-black patch on the ventral surface as noted by McKenzie and Keenleyside (1970), remnants of which were detectable through the year after its original appearance.

Time of Spawning

The first spent females were observed on June 6 with no great increase in percentage frequency of occurrence until mid-July. By the end of July, all but one of 38 fish were spent, and that one was partly spent. It appears that the spawning season for these fish is approximately 8 wk long. Equally long spawning periods are reported by Nelson (1968b) and Bigelow and Schroeder (1953).

Spawning Habitat

The spawning act was not observed in the lake, therefore the exact location and spawning substrate cannot be identified. McKenzie and Keenleyside (1970) saw Lake Huron *Pungitius* spawning among rocks around the shore. No such activity was noted in superficial observation in the Apostle Islands. Ripe station 3 females and males displaying vivid reproductive coloration were found exclusively in the dense growth of *Nitella* sp. At station 2, ripe fish of both sexes were collected over highly organic

muds 12 to 24 fathoms deep, and Lake Superior *Pungitius* spawned successfully in this mud in the laboratory while no spawning resulted in rocky or sandy substrates (Griswold and Smith, 1972).

Fecundity and Egg Size

On 27 June 1969, stickleback samples at station 2 and 3 contained a large proportion of females which were in Stage IV of maturity. These fish were used in the analysis of fecundity. A total of 72 fish were examined from station 2 and 60 from station 3 (Table 14).

Several authors have found a high percentage of atresia in maturing eggs of a number of species. This may cause an overestimate of fecundity (Wagner and Cooper, 1963; Vladykov, 1956; Wydoskii and Cooper, 1966). To determine if appreciable atresia occurred in stickleback eggs, the number of eggs in the 132 ripe fish were compared to egg numbers in fish taken from the same stations about 3 wk prior to spawning (Table 15). Analysis of covariance (Snedecor, 1956) revealed egg numbers in the "green" fish were significantly greater (0.01 level) than those in corresponding size of ripe fish ($F_{1,29} = 7.67$). It appears atresia occurs in maturing ninespine stickleback eggs just prior to spawning. Eggs which appeared to be degenerating after some maturation were almost always present in maturing ovaries. The decrease in egg number at each length interval presented in Table 15 ranged from 24 to 39%. The amount of atresia was not dependent on fish size. Vladykov (1956) estimated atresia affected up to 60% of maturing eggs in natural brook trout populations. It is generally agreed that atresia is a physical reaction to the pressure caused by the growing ovary (Vladykov, 1956).

When means of ripe egg numbers at each millimeter body length interval were plotted for stations 2 and 3 ninespine sticklebacks, linear relationships were implied (Figure 8). Least squares equations which describe the lines were:

$$\text{Station 2} \quad Y = -79.75 + 2.37X$$
$$\text{Station 3} \quad Y = -67.81 + 2.12X$$

where Y = number of eggs and
X = length of fish in millimeters.

TABLE 14.—Average number of eggs counted from 132 ninespine sticklebacks of various lengths collected 27 June 1969.

	Station 2			Station 3		
Length (mm)	Mean number eggs	Mean fish weight (g)	Number of fish	Mean number eggs	Mean fish weight (g)	Number of fish
55	—	—	0	84.0	1.217	1
56	—	—	0	—	—	0
57	—	—	0	—	—	0
58	—	—	0	65.0	1.407	1
59	—	—	0	75.0	1.453	1
60	—	—	0	—	—	0
61	—	—	0	—	—	0
62	—	—	0	61.0	1.662	1
63	86.0	1.844	2	59.5	1.737	2
64	—	—	0	68.0	1.712	1
65	74.3	1.827	3	77.7	2.013	6
66	76.0	1.896	3	69.8	1.901	4
67	78.8	1.997	10	71.0	2.101	4
68	82.7	2.031	6	73.0	2.206	4
69	76.8	1.961	5	78.3	2.288	6
70	86.6	2.142	5	87.7	2.371	7
71	82.8	2.254	4	71.3	2.544	3
72	93.4	2.429	7	104.0	2.452	2
73	103.2	2.639	5	82.6	2.766	5
74	98.3	2.400	3	90.0	2.730	7
75	88.0	2.742	5	85.5	2.920	2
76	113.8	2.942	7	94.0	2.776	1
77	112.3	2.990	3	—	—	0
78	95.7	3.070	3	—	—	0
79	—	—	0	103.0	2.962	1
80	103.0	3.010	1	—	—	0
81	—	—	0	98.0	3.522	1

TABLE 15.—Comparison of mean number of eggs per female in fish taken in early June 1970 about 3 wk prior to spawning and fish which were in "running-ripe" condition.

Fish length (mm)	"Green" fish	"Running-ripe" fish
58	—	65.00
59	—	—
60	—	—
61	82.00	—
62	88.50	61.00
63	99.00	72.75
64	98.66	68.00
65	99.62	76.56
66	99.33	72.45
67	116.80	76.57
68	114.50	78.82
69	114.66	77.61
70	114.00	87.24
71	124.25	77.87
72	137.75	95.75
73	126.00	94.70
74	130.66	92.49
75	128.00	87.28
76	132.00	111.32
77	—	112.30
78	158.00	95.70
79	—	103.00
80	—	103.00
81	—	98.00
Total fish	58	132

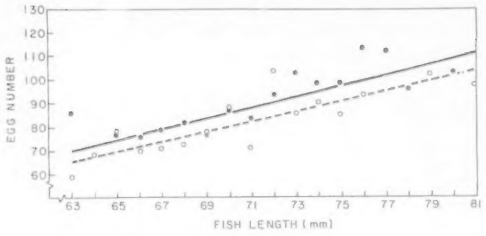

FIGURE 8.—Least squares regression lines indicating the relationship between fish length and number of eggs. Solid line and dots, station 2; dashed line and open circles, station 3.

Coefficient of determination (r^2) values were 0.71 and 0.72 for stations 2 and 3 respectively.

Differences in fecundity relationships between the two stations were implied and analysis of covariance revealed a significant difference (0.01 level) in elevation of the two regressions ($F_{1,28} = 19.0$). With the presence of atresia, the most obvious theory for this difference would be a slight difference in time of spawning at the two stations. This is suggested by the slightly smaller mean weights of female fish from station 2 sticklebacks at the time of these ovary collections (Table 14). This could be interpreted to mean station 2 females had not matured as much as station 3 fish since female sticklebacks increase their weight by as much as 10% during the maturation period. Atresia would then have acted on the station 2 fish to reduce their fecundity. Any difference in spawning time is probably related to environmental differences between the stations, exemplified by the presence of rooted aquatics at station 3 and their apparent absence at station 2.

Measurements of egg size of six *P. pungitius*, 62-79 mm long, were made on eggs deposited in laboratory aquaria, since Vrat (1949) found stickleback eggs reached maximum size only on extrusion into the water. Eggs were left in the water about 15 min before they were removed and measured under a binocular microscope equipped with an optical micrometer. Egg size appeared to be rather constant with no relationship to size of fish. Egg diameter ranged from 1.53 to 1.98 mm ($\bar{x}$ = 1.76 mm).

Mean weight of ovaries containing ripe eggs was 10.2% and 9.8% of mean fish weight at stations 2 and 3, respectively. Since ovaries in immature fish are very small and some somatic growth had already taken place by spawning time, it is clear that gonad maturation requires a gain in weight of over 10% of the winter weight of the fish. However, early somatic growth in mature females is considerably less than in males (Table 7). It appears that most early annual weight gain in females goes into egg production and rapid somatic growth does not occur until after spawning.

Sex Ratio and Sex Specific Mortality

The sex ratio of sticklebacks was determined for various years of life and for various months because it was obvious from general observation that females predominated in the samples. All 808 fish from which otoliths were extracted were used in the sex ratio calculations. The ratios were:

Age-group	*Male:Female*	*Chi-square*
0	0.930:1	10.54 (7*df*)
I	.809:1	.68 (4*df*)
II	.339:1	22.19 (3*df*)**
III	.125:1	20.57 (3*df*)**
IV	all female	

The χ^2 values for age-groups II and older were significant at the 0.01 level, indicating the ratios were significantly different from 1 to 1.

The sex ratios by month of all fish 1+ and older beginning in April were:

Month	*Male:Female*
April	0.692:1
May	.714:1
June	.366:1
July	.197:1
August	.211:1
November	.137:1
December	.100:1

Monthly length-frequency histograms (Figures 5-6) indicate the presence of two distinct age-groups in most months, the older fish being strung out in an uneven pattern beyond the

second mode. However, the second mode disappeared in August as young-of-the-year began to appear in the catches. Since the 2-yr-old fish, which remained after August were predominantly female (Table 16), it appeared the die-off among old fish, as indicated by length-frequency diagrams, was more prevalent among males. The monthly sex ratios of the age-groups comprising most of the spawning population seemed to indicate that such mortality began to occur as early as June with a sharp drop in males in the catchable population through July. However, the die-off did not appear in the length-frequency diagrams until August. This discrepancy might be explained by a differential movement of males onto the spawning grounds in June to set up their territories and/or an increased awareness of the fishing gear by territorial males. Both these explanations could result in decreased male availability to the trawl during the spawning period. However, after the spawning period, males remained low in the catch throughout the rest of the year, indicating a high mortality among males which spawned.

These interpretations are strengthened by two other observations. Males which had spawned previously were identifiable at any time by vestiges of spawning colors on their ventral surface. Few of these individuals were seen in the collections. Also, in a laboratory experiment described by Griswold and Smith (1972), eight males brought off broods to the point where fry were actively swimming about in the aquaria. Seven of these males died within a month of spawning. There was no mortality observed among 10 females which spawned in the laboratory.

TABLE 16.—Ratio of male sticklebacks to females of different age-groups in various months. Annulus formation is complete after July.

Age	Apr.	May	June	July	Aug.	Nov.	Dec.	Mean[1]
0	0.5	1.2	0.7	—	2.0	0.9	0.5	0.9
1	.7	1.1	.2	0.3	.6	.9	1.6	.8
2	.3	.3	0	.1	.2	.4	.4	.3
3	0	0	0	.1	0	.1	.3	.1
4	—	—	0	0	—	—	0	0
Mean[2]	.4	.7	.3	.2	.7	.7	.7	

[1] Weighted for number of fish in each month.
[2] Weighted for number of fish in each age-group.

PARASITE INFECTION

The pleurocercoid stage of the cestode, *Schistocephalus pungitii* Dubinina (Pavlovskii, 1964), is the only parasite generally abundant among ninespine sticklebacks. The procercoid infects numerous species of copepods, and when these are eaten by sticklebacks, the procercoid burrows through the stomach wall to grow as a pleurocercoid in the body cavity. At this stage the parasite is species-specific as, so far as is known, it attacks only the ninespine stickleback. Two months are required for full growth of the pleurocercoid, at which time it may infect a number of fish-eating birds. No other stickleback parasites were noted in the study.

Rate of infection in Apostle Islands sticklebacks was low in 621 fish examined. Only 4 of 362 fish (1.10%) were infected prior to 1 August in all years of the study combined, and 13 of 259 fish (5.01%) were infected after 1 August. Summer and fall infection would intuitively be higher because of greater copepod abundance at that time. The largest pleurocercoid found was 22 mm long and weighed 0.225 g or 14% of the host's weight. Two fish had two pleurocercoids each which made up 18 and 14.5% of the fish's weight, respectively. These parasites were found in 7 male and 10 female sticklebacks. Fish infected at spawning time did not appear to be maturing.

FOOD HABITS OF THE STICKLEBACK AND ASSOCIATED SPECIES

Five papers mention the food of *P. pungitius*. Forbes (1883) found two specimens which contained equal amounts of diptera larvae and cladocerans. Blegvad (1917) found copepods and stickleback eggs predominant in 112 Danish fish. Hynes (1950) reported cladocera, amphipods, and chironomid larvae were the most important food items in fish from an English stream. Bigelow and Schroeder (1953) state that the stickleback feeds voraciously on fish eggs and fry and can be very destructive to other species in fresh water. Anderson and Smith (1971) report crustaceans make up more than 90% of the Lake Superior stickleback diet. In the present study, emphasis was placed on the food

habits of sticklebacks and several associated species with which they are most likely to compete or which may be involved in predator-prey relationships with sticklebacks.

In the stomach analyses, contents were removed from the upper esophagus to pyloric sphincter and measured by water displacement in 15-cm³ centrifuge tubes. The contents were then emptied into a gridded petri dish for indentification under a binocular microscope at 10× magnification. Organisms present in small numbers were counted, but larger numbers were estimated from counts in randomly selected squares of the dish. Percentage of each item in the total volume of each stomach was estimated. The data are reported as percentage frequency of occurrence and percentage of total volume for each food item in stomachs containing food.

Invertebrate Abundance

Invertebrates important in the stickleback diet were sampled with the mysis sled concurrently with sticklebacks used in food analysis; therefore, it is assumed that the gear sampled food organisms that were available to sticklebacks. One-mile tows were made with the sled and the invertebrate catch was preserved in 10% Formalin. Invertebrate samples were identified and enumerated on a gridded petri dish in the same manner as stomach contents.

The average number of organisms per 100 m of tow is shown in Table 17 for 18 tows on five dates. The data indicate the extreme abundance of *Pontoporeia affinis* adjacent to the bottom. Although copepods were also abundant, they were usually not as important in mass as either *Pontoporeia* or *Mysis*. Coregonid eggs and fry were found occasionally in fall plankton samples.

Food of the Stickleback

Food analyses of 421 stickleback stomachs in nine different months were made (Table 18).

Fish under 50 mm long fed primarily on *Pontoporeia* and copepods, which made up 79 and 13% of the total food volume, respectively. Cladocerans were of minor importance, and mysids were also present infrequently. Other organisms present in these smaller fish were chironomid and diptera larvae and a filamentous green alga.

Food of sticklebacks 50 mm and over were characterized by a variety of larger food items, suggesting that one factor limiting the diet of young fish is size of food items. *Pontoporeia* taken by the under 50-mm sticklebacks were small in size (4.0 mm average) compared with those found in adult stomachs (6.5 mm).

In these larger fish, *Pontoporeia* made up 61% of the total stomach volume, *Mysis* 21%, copepods 8%, and miscellaneous other items 10%. *Pontoporeia* was the major food item in all months but November. There is a suggestion from late fall and early spring samples that coregonid eggs may be an important food item in the winter. Except for these eggs, there is little to suggest that *P. pungitius* is significantly

TABLE 17.—Average number of invertebrates caught per 100 m in tows along bottom with mysis sled in the Apostle Islands.

[The percentage volume of each item found in stickleback stomachs is in parentheses.]

Organism	29 Apr. 1968	22 July 1968	13 Nov. 1968	29 Apr. 1969	27 June 1969
Number of tows	4	3	4	2	5
Amphipoda:					
Pontoporeia affinis	437,750 (88)	748,260 (61)	117,600 (33)	32,360 (84)	371,660 (69)
Mysidacea:					
Mysis relicta	120 (4)	6,110 (12)	34,280 (60)	1,370 (8)	320 (9)
Cladocera	3,170 (1)	1,040 (4)	280 (0)	30 (2)	2,610 (3)
Bosmina spp.	2,210	910	190	30	2,330
Daphnia spp.	920	120	90	0	90
Others	40	10	0	0	140
Fish eggs	0 (0)	0 (0)	0 (0)	0 (6)	0 (0)
Copepods	43,460 (7)	98,630 (23)	47,210 (0)	23,500 (0)	199,790 (16)
Diptera larvae	0 (0)	0 (0)	0 (6)	0 (0)	0 (3)
Mollusca					
Sphaeriidae	2 (0)	0 (0)	0 (0)	1 (0)	0 (0)
Other	0 (0)	0 (0)	0 (1)	0 (0)	0 (0)

TABLE 18.—Food of Apostle Islands sticklebacks expressed as percentage frequency of occurrence and (in parentheses) percentage of total volume for each food item.

Stickleback length	Item	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Under 50 mm	Number of Stomachs	0	0	13	18	4	0	5	14	0
	Number empty	0	0	2	1	0	0	0	0	0
	Crustaceans:									
	Pontoporeia affinis			62 (66)	100 (99)	100 (100)			93 (86)	
	Copepoda			15 (11)				100 (97)	7 (3)	
	Cladocera							20 (3)		
	Mysis relicta				6 (1)				7 (7)	
	Insects:									
	Chironomidae			8 (9)					14 (4)	
	Diptera									
	Algae			8 (9)						
50 mm and over	Number of stomachs	31	66	99	27	27	55	20	20	22
	Number empty	11	4	3	3	0	1	1	0	2
	Crustaceans:									
	Pontoporeia affinis	80 (75)	61 (49)	90 (75)	30 (24)	92 (92)	82 (62)	90 (80)	60 (30)	59 (45)
	Hyallela sp			1 (1)						
	Mysis relicta	5 (1)	56 (42)	30 (8)	11 (10)		44 (30)	25 (1)	70 (65)	36 (32)
	Copepoda	5 (2)	12 (3)	8 (13)	52 (38)	4 (2)	5 (1)	5 (12)		
	Cladocera	5 (2)		1 (1)	33 (9)	11 (6)	2 (1)	5 (2)		
	Insects:									
	Chironomidae			9 (1)	11 (5)		16 (3)			
	Other Diptera			2 (1)	7 (6)	4 (1)				
	Ephemeroptera		1 (1)							4 (3)
	Nemotoda						2 (1)			
	Coregonid eggs	5 (2)	12 (3)							27 (20)
	Unidentified	5 (15)	1 (2)	3 (2)	7 (7)		22 (3)	5 (5)	5 (5)	

destructive to fish eggs and fry in Lake Superior as Bigelow and Schroeder (1953) thought was generally the case. Neither eggs nor fry of any other kind were found in stickleback stomachs, although gravid females and young-of-the-year of smelt, trout-perch, slimy sculpins, and pygmy whitefish were taken in the same areas at about the same time as the stickleback stomach samples.

The percentage volume of total stomach contents for each day and for each food item taken in the mysis sled is given in Table 17. *Pontoporeia* was the most important food item except in the November sample. In that month, mysids were the most important food and were more abundant in plankton samples than at any other time. Copepods were most abundant in the June and July samples, and their relative contribution to stickleback diet was also highest in these months. In general, when mysids or copepods became relatively more abundant with respect to themselves or to other zooplankters in the plankton samples, they also become more important in the stickleback diet. This suggests that the stickleback shows no strong food preferences but is adaptable and eats what is most available.

Relation to Food Utilization of Other Forage Species

Juvenile smelt (less than 12.5 cm), trout-perch, and slimy sculpins were found to have diets similar to sticklebacks in Lake Superior (Anderson and Smith, 1971). Since all these species were common in the Apostle Islands, competitive relationships between them and the stickleback could exist. A rank correlation coefficient was used to measure the similarity of food composition between two samples and thus permit examination of interspecific and intraspecific feeding relationships.

Table 19 is an example of the computation as discussed by Snedecor (1956). In the case of

TABLE 19.—An example of the calculation of rank-correlation coefficients.

Food item category	10 stickleback rank	10 trout-perch rank	Difference d	d^2
Pontoporeia	1	1	0	0
Mysis	3	4	−1	1
Copepods	2	3	−1	1
Chironamidae	5	2	+3	9
Cladocera	4	5	−1	1

$n = 5 \qquad \Sigma d = 0 \qquad \Sigma d^2 = 12$

$$\bar{r_s} = 1 - \frac{6(12)}{5(25-1)} = 1 - \frac{72}{120} = 0.40$$

a tie in importance of any two categories, the larger item was ranked first. An r_s value of +1.0 indicates that the various food categories were eaten in the same order of preference, and as r_s approaches −1.0, there is no agreement in order of occurrence.

To test the hypothesis that fish of the same species eat the same things in different areas, 10 randomly selected fish caught from one station within 3 days were compared. In interspecific tests, 10 fish of each species taken at the same station on the same day were used. Except for smelt, only adults were used in the tests because juveniles of other species were not completely available to the gear and not taken in large enough quantities to test.

Analyses of individual tests were not made; instead the results from several comparisons (N in Table 20) were combined and a test made using the combination of probabilities discussed by Snedecor (1956:216). The sum of the natural logarithms of the probabilities associated with each of several comparisons is multiplied by −2, and the resulting values have a chi-square distribution with two degrees of freedom for each comparison. Pearson (1924) presents a figure which allows graphical calculation of probabilities associated with r_s.

Intraspecific correlations were significant for all comparisons (Table 20). Indications are that food habits among individuals of the same species were almost identical within the Apostle Islands.

Significant interspecific correlations were found between sticklebacks and slimy sculpins in spring and summer and sticklebacks and

TABLE 20.—Food composition similarity measured by rank-correlation coefficients (r_S) between sticklebacks and other Apostle Islands species. (N equals the number of individual tests for each comparison, and n equals the number of food categories in each comparison.)

Comparison	N	n	Mean r_S	Chi-square
1. Between adult sticklebacks of stations 2 and 3	5	6	+0.94	36.89**
2. Between adult trout-perch from two stations	3	5	+.83	16.81*
3. Between juvenile smelt from two stations	3	4	+.85	16.98*
4. Between adult sculpins from two stations	5	6	+1.00	—
5. Between adult sticklebacks and other species within each catch:				
Spring:				
Trout-perch	7	5	+.70	30.89*
Smelt	10	4	+.40	34.29
Sculpins	10	6	+.89	62.02**
Summer:				
Trout-perch	4	5	+.43	13.94
Smelt	2	4	−.30	6.54
Sculpins	10	6	+.89	62.02**
Fall:				
Trout-perch	4	5	+.33	13.28
Smelt	4	4	+.40	13.72
Sculpins	5	6	+.37	16.87

* Significant at the 0.01 level.
** Significant at the 0.005 level.

trout-perch in spring. The significant rank correlation does not necessarily indicate the amount of competition for food, but merely the potential for such competition. For competition to occur, there must be a demand by more than one organism for the same food in excess of immediate supply. It can only be said that since the abundance of sticklebacks and slimy sculpins are positively correlated in the index catches and their food relationships are similar, the possibility of competition between the two species exists during some seasons. The actual existence of competition is highly questionable because of the apparent abundance of *Pontoporeia*, the number one food item, and the apparent adaptability of the stickleback in food utilization. The drop in correlation in the fall was due to greater use of chironomids by sculpins.

While the correlation with trout-perch also indicates potential competition for food, their abundance in the index trawl samples was negatively correlated and Dryer (1966) found trout-perch and sticklebacks to have different bathymetric distributions. While the trout-perch and sticklebacks utilized the same foods in spring, their secondary foods were different in summer and fall. Anderson and Smith (1971) found trout-perch fed on wider variety of food items than sticklebacks in the Apostle Islands. This combined evidence seems to indicate that competition between these two species is also unlikely.

Sticklebacks as Forage for Other Fish

Several fish species which occur in Lake Superior have been reported to feed on sticklebacks at various locations. These include lake trout; brown trout, *Salmo trutta* L.; rainbow trout, *Salmo gairdneri* Richardson; burbot, *Lota lota* (L.); and various sculpins. Of these, the lake trout was the only species which fed heavily on sticklebacks in the Apostle Islands.

Dryer, Erkkila, and Tetzloff (1965) related a change in diet in juvenile Lake Superior lake trout to their size. The diet, primarily a crustacean-insectivorous type in small trout, became piscivorous in larger fish.

In the present study, sticklebacks were found in 7.5% (33) of 436 lake trout less than 28 cm (11 in.) long (TL). Only 3.5% of the volume of stomachs from 142 fish under 25.4 cm (10 in.) was sticklebacks. In 294 trout from 25.4 to 28.0 cm, sticklebacks made up 32% of the volume of the diet.

Sticklebacks were a major part of the diet of lake trout from 28.0 to 38.0 cm (11.0 to 14.9 in.) (Figure 9). *P. pungitius* made up 39% of volume in the diet and were found in 42% of the 176 trout which contained food. Smelt was the second most abundant fish species in the diet of 28- to 38-cm trout. The food habits of trout remained about the same for all ice-free months (Anderson and Smith, 1971).

The major food of trout longer than 38 cm was smelt. Of 30 trout in this size range, 69% of the stomach contents were smelt remains. Sticklebacks were found in five of these fish and made up 17% of the volume. Nineteen adult sticklebacks and two sculpins were found in one 50-cm (19.7 in.) trout. Sticklebacks eaten by trout were all age-group I or older. No stickleback eggs or age-group 0 fish were found in over 4,500 trout stomachs sampled on the Lake Superior project.

The explanation of the absence of small sticklebacks in the trout diet is probably one of dis-

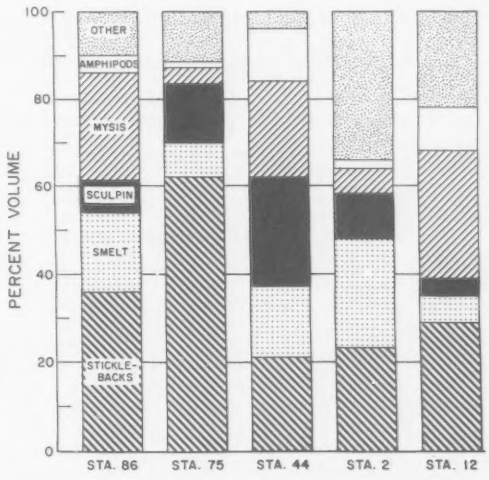

FIGURE 9.—Percent volume of various food items found in lake trout 28 cm and longer at various sampling stations in the Apostle Islands. Fish were taken in June and September during the two annual BCF index trawling cruises.

tribution. After hatching, the young sticklebacks congregate in the shallow sandy areas where they are unavailable to lake trout and most other species. By the time they leave the shallow water in late fall, they have grown to 45 mm or more. It is at this length that they begin to appear in trout stomachs the following spring.

Smaller trout cannot feed well on sticklebacks once the latter become available after a summer's growth, because of the protective spines. This inability explains the relative unimportance of sticklebacks in the diet of small trout. Similarly, Hoogland, Morris, and Tinbergen (1957) found young northern pike, *Esox lucius* L., rejected sticklebacks, first exhibiting a negative reaction to mechanical stimuli upon contact with the spines and then a visual avoidance. Upon reaching a certain size, the pike preferentially take sticklebacks (Frost, 1954). A discussion by Fortunatova (1959) supports this theory. The dietary shift to smelt by larger trout can be explained by assuming the optimum size of the prey increases as the trout grow larger.

Compared to all lake trout over 28 cm long taken from a number of trout index stations, fish from stations 75 and 86 ate a high percentage of sticklebacks (Table 21, Figure 9). At station 86, considered the best trout nursery area in the Apostle Islands, sticklebacks were the predominant food item even though juvenile smelt were more abundant in the index trawl samples (Table 9). At station 75, the second most important nursery area, sticklebacks were very abundant, and they made up more than 60% of the trout diet. Station 12 sticklebacks and smelt were about equal in the index catch, but sticklebacks were much more important in the trout diet. At station 44, the predominant forage fish in the trawl samples was sculpins, and these were dominant in trout stomachs. At this station, sticklebacks were comparatively rare in occurrence, but still made up 21% of the volume of the trout diet. It might be assumed from station 44 data that sculpins are an important item in the diet and that trout will substitute sculpins when sticklebacks and smelt are not readily available. However, the stations with high sculpin abundance relative to stickleback abundance do not support large numbers of trout. From these data, it appears that the availability of sticklebacks at the various stations is probably important in the selection of these areas by lake trout as

TABLE 21.—Percent frequency of occurrence and (in parentheses) percent total volume for each food item found in lake trout 28 cm and longer at various sampling stations in the Apostle Islands. Fish were taken in June and September during the two annual Bureau of Commercial Fisheries index trawling cruises.

Item	Station 86	Station 75	Station 44	Station 2	Station 12
Number of stomachs	77	45	24	51	33
Number empty	20	3	0	0	0
Crustaceans:					
Mysidacea	35 (25)	15 (4)	33 (22)	16 (6)	64 (29)
Amphipoda	18 (4)	8 (<1)	17 (12)	2 (<1)	36 (10)
Copepoda	—	1 (<1)	—	—	3 (<1)
Fish:					
Smelt	14 (18)	9 (8)	12 (16)	21 (25)	6 (6)
Stickleback	30 (36)	64 (62)	17 (21)	21 (23)	33 (29)
Sculpin	6 (7)	13 (13)	21 (25)	12 (10)	6 (4)
Unidentified	9 (8)	15 (11)	17 (3)	27 (36)	24 (19)
Fish eggs	—	—	—	1 (<1)	—
Insects:					
Chironomidae	6 (<1)	6 (<1)	2(<1)	—	3 (<1)
Coleoptera	1 (<1)	—	—	—	—
Trichoptera	1 (<1)	1 (<1)	—	—	—
Other	1 (<1)	7 (<1)	—	1 (<1)	6 (3)
Miscellaneous	—	1 (<1)	—	—	—

nursery areas, although other factors are also important because there are many areas where sticklebacks are abundant and trout are not. Conversely, no good trout nursery area are known where sticklebacks are not abundant.

The importance of the stickleback as a food item for the lake trout in the Apostle Islands appears to be substantial while the latter are between 28 and 38 cm long. No information is available, however, to indicate the amount of substitution which would occur if the sticklebacks were less available.

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ABUNDANCE AND SIZE OF JUVENILE SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, AND ASSOCIATED SPECIES IN LAKE ALEKNAGIK, ALASKA, IN RELATION TO THEIR ENVIRONMENT[1]

DONALD E. ROGERS[2]

ABSTRACT

Juvenile sockeye salmon, *Oncorhynchus nerka*, and associated fish in the littoral of Lake Aleknagik (Bristol Bay, Alaska) were sampled systematically from spring to midsummer (1962-72) with a beach seine. Apparent mortality rate and relative abundance were estimated from catches. Juvenile sockeye salmon and threespine stickleback comprised the majority of the population, and slimy sculpin, ninespine stickleback, and Arctic char fry the remainder. The annual abundance of juvenile sockeye salmon was related to the abundance of parent spawners. No correlation was evident among the annual estimates of abundance of the five species.

Age was determined from length-frequency distributions, and growth rates were calculated for sockeye salmon (age 0), Arctic char (age 0), and threespine stickleback (age I). The mean lengths of sockeye salmon fry and char fry on 20 June were positively correlated with water temperature, whereas the mean length of threespine stickleback (age I) on this date was inversely correlated with the average catch of sockeye salmon fry in the previous year. The mean lengths of all species on 20 July were inversely correlated with the mean catch of sockeye salmon fry. A limited capacity of the Lake littoral to sustain growth of individual fish was indicated.

The annual commercial catch of anadromous sockeye salmon, *Oncorhynchus nerka* Walbaum, from the Nushagak District of Bristol Bay declined from an average of about 5 million fish in the early 1900's to only about 1 million in recent years (Mathisen, 1971). Since the early 1950's, the Fisheries Research Institute has studied the freshwater life of the stock to understand the factors controlling the average abundance and annual variation in abundance of the adult run. We have assumed that a significant portion of the variation is related to the variation in abundance and growth of juveniles, especially fry (age 0), and have concentrated effort on the Wood River lake system because it has been the major producer among the river systems in the District (Figure 1).

The sockeye salmon fry inhabit different parts of each lake from spring to fall. From mid-May to mid-June, when the ice breaks up, to mid-July, they reside along the shore and in shallow bays; in mid-July they begin to move offshore; and from mid-August through September they occupy the pelagic areas (Burgner, 1962). Accordingly, the populations are sampled during early summer through beach seining and during August and September through townetting and echo sounding (Rogers, 1967). Beach seine sampling has been conducted throughout the District but has been concentrated in Lake Aleknagik. The catch and length statistics for sockeye salmon fry from an extensive effort in the lake in 1962 were analyzed by Pella (1968), and the catch statistics for five species of fish from 1964 through 1966 were examined by Waters (1969).

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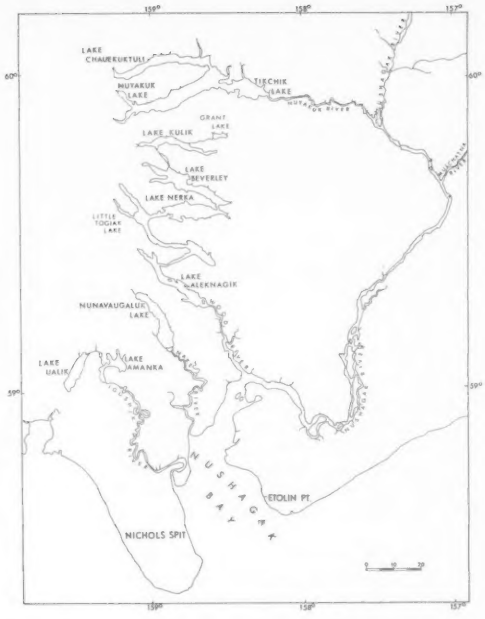

FIGURE 1.—The Wood River lake system and adjoining river systems in the Nushagak District, Bristol Bay, Alaska.

The primary objective in beach seine sampling has been to obtain periodic estimates of fish length in early summer. The secondary objectives have been (1) to estimate the annual relative abundance and growth of fish species associated with juvenile sockeye salmon to determine the effect, if any, that they may have on survival and growth of juvenile sockeye salmon and (2) to determine the relationships among relative abundance of sockeye salmon fry, abundance of parent spawners, and abundance of returning adult sockeye salmon. The data and statistical tests are detailed in Rogers (1972). The purpose of this report is to examine the relationships among annual estimates of the size and abundance of fish and the physical parameters of the environment during early summer.

MATERIALS AND METHODS

A detailed description of the gear and sampling procedures is given by Waters (1969). The seine used was 35 m in length and had a midsection of 6-mm mesh, 7.6 m long and 3.7 m deep. A 1.8-m bridle and a 17-m hauling rope were attached to each end of the net. The seine was set in a semicircle about 15 m from shore and hauled by hand, usually by two men. Catches consisting of less than 500 fish were preserved in 10% Formalin.[3] Larger catches were successively divided in half until approximately between 200 and 500 fish remained. These were preserved, and the fraction taken was recorded. For each haul the date, time, location, set direction, and surface water temperature were noted. Other physical parameters measured in connection with the beach seining were the date of ice breakup, lake level, and solar radiation.

In 1962, beach seine hauls were made at 24 stations on Lake Aleknagik in eight time periods between 20 June and 8 September. In 1963, nine of the stations were sampled on 24 July and 3 August. From 1964 through 1972, generally 10 stations (Figure 2) were sampled at five weekly intervals between 22 June and 23 July and once between 2 to 5 August. Seining was conducted at the 10 stations between 0930 and 1600 h, seldom during rough water conditions, i.e. when there were waves on shore. A description of the beach seine stations is given in Rogers (1972).

Between 1 and 7 days after collection, the fish were enumerated and measured to the nearest millimeter from tip of snout to end of middle ray of the tail. In 1962 only juvenile sockeye salmon and threespine stickleback, *Gasterosteus aculeatus* Linnaeus were measured, whereas in the remaining years fish of all species were measured. Also, only 50 sockeye salmon fry were measured in samples containing more than 75 sockeye salmon fry, and only 200 threespine stickleback were measured in samples containing over 250 of this species.

The length frequencies were plotted by species and lake area (Figure 2) and for areas combined. Partial age compositions were determined from the length frequencies, and mean lengths were calculated for those age groups

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

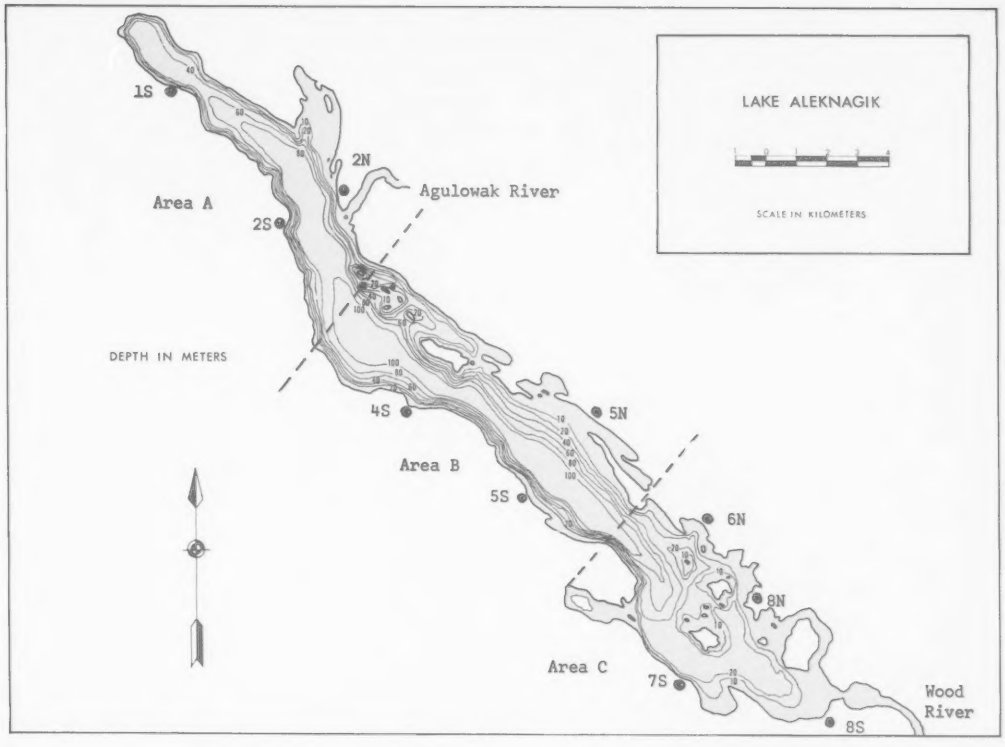

FIGURE 2.—Beach seine stations and lake sampling areas in Lake Aleknagik.

that were easily separated from the length frequencies. The mean lengths were converted to equivalent live lengths so as to adjust for the shrinkage due to preservation (Rogers, 1964). These were plotted by date and examined for determination of the most suitable growth model. A curvilinear relationship was indicated, and regressions of natural logarithm (ln) mean length on coded date (1 June = 1, 1 July = 31, etc.) were calculated through weighting the observations with geometric mean catch. A weighting procedure was used because (1) variance of the means tended to increase during the season as a result of the decline in catch (hence sample size) and (2) the accuracy of mean lengths from beach seine samples as estimates of mean length in the population tended to decrease in midsummer as the fish moved offshore. Annual growth rate and fish size in given periods were estimated from the regressions.

The beach seine catch data were analyzed through logarithmic transformation. An analysis of variance was conducted with the catches made in the first four periods of sampling (20 June-19 July) for the purpose of determining the significance of observed variation associated with location (station and lake area), date, and year. The last two periods (21 July-5 August) were excluded from the analysis since the catches of sockeye salmon fry in these periods were obviously lower than those in the other periods and age 0 fish of the longer lived species often appear at this time.

Mortality rate in a population is estimated commonly from changes in catch with time when catch per unit of effort can be reasonably assumed to be proportional at all times to true

TABLE 1.—Dates of ice breakup, surface water temperatures, and relative lake levels during beach seine sampling in Lake Aleknagik, 1962 through 1972.

Year	Date of ice breakup	Mean surface water temperature (°C)			Mean lake level (cm)		
		20-24 June	20 June-19 July	21 July-5 August	21-25 June	21 June-20 July	21 July-5 August
1962	1 June	9.0	11.8	12.0	157	137	89
1963	2 June	—	11.1	12.3	140	122	80
1964	15 June	7.7	9.4	11.6	150	139	82
1965	5 June	7.4	7.0	11.7	184	147	97
1966	6 June	7.6	8.5	12.8	157	148	112
1967	28 May	9.0	12.1	13.9	146	118	68
1968	31 May	10.8	13.3	14.9	102	84	50
1969	2 June	9.4	10.8	12.5	220	168	92
1970	23 May	7.8	9.8	11.2	154	134	109
1971	16 June	8.5	10.0	9.4	177	148	167
1972	8 June	4.3	7.5	12.0	191	171	108

population size. A frequent source of error is the variation in availability of the fish population to the sampling net. Beach seine catches of sockeye salmon fry and threespine stickleback decline seasonally as a result of movement offshore and mortality. Apparent mortality rates were estimated from linear regressions of ln mean catch on coded date.

The data were examined through stepwise multiple regression and linear correlation techniques for determination of significant relationships among the physical and biological parameters.

RESULTS

Climatological observations for the Wood River lake system are given in Rogers, Siler, and Croker (1970). The average date of ice breakup from 1951 to 1972 is 1 June, and the range in dates is from 14 May to 16 June. A summary of physical data collected in connection with the beach seine sampling in Lake Aleknagik is given in Table 1. Lake level usually rises rapidly after ice breakup until mid-June and declines through the summer. Inshore surface water temperatures rise gradually from ice breakup to late July and then level off. Water temperatures are lower on the average in the upper third of the lake (area A) than elsewhere. From 1962 to 1972 the average surface water temperatures during 20 June-19 July were 9.1°, 10.3°, and 10.7°C in areas A, B, and C, respectively.

Fish of 24 species have been collected in Lake Aleknagik, but only juvenile sockeye salmon and threespine stickleback have been greatly predominant in beach seine catches (Table 2). These two species are also the only ones that become pelagic in midsummer. Three other species appear in significant numbers in the catches: ninespine stickleback, *Pungitius pungitius* Linnaeus; slimy sculpin, *Cottus cognatus*

TABLE 2.—Sums of geometric mean beach seine catches of five fish species by lake area, Lake Aleknagik, 1962 through 1972.

	Area	Sockeye salmon		Threespine stickleback	Ninespine stickleback	Sculpin	Char fry	Sum
		Fry	Fingerling					
20 June-19 July								
	A	258	1	130	8	43	15	455
	B	265	2	303	11	25	2	608
	C	86	8	160	22	23	1	300
	Total	192	3	184	12	29	4	424
21 July-5 August								
	A	36	1	132	13	23	8	213
	B	20	2	75	7	8	3	115
	C	20	2	92	14	10	2	140
	Total	24	2	97	11	12	3	149

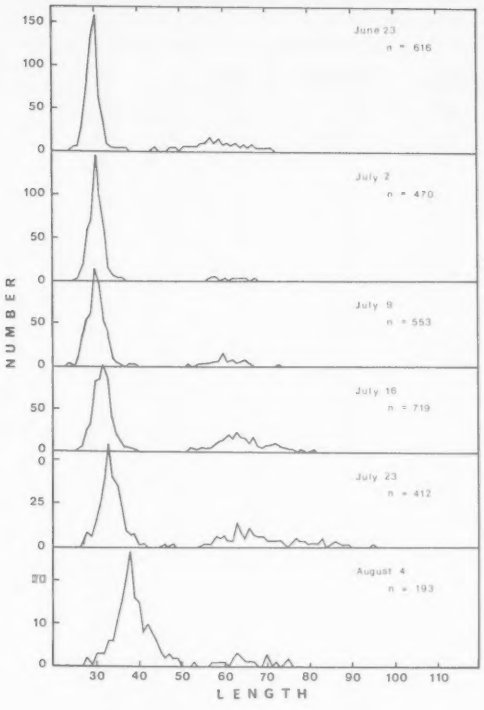

FIGURE 3.—Length-frequency distributions (mm) of sockeye salmon, 1966.

Richardson; and Arctic char fry, *Salvelinus alpinus* Linnaeus. Of primary value in the beach seine statistics are the annual estimates, since our main concern is with the source of the observed annual variation in adult sockeye salmon abundance. Geographical and temporal variations were examined and are discussed here to the extent necessary for procurement of valid annual estimates of abundance, growth and size.

Sockeye Salmon

Length-frequency distributions for juvenile sockeye salmon are shown in Figures 3 and 4 for a year in which growth was below average (1966) and a year in which growth was above average (1968). The length frequencies are based on number of fish measured and thus do not reflect variation in abundance among time periods and years. The apparent abundance of sockeye salmon fingerlings in comparison to fry is exaggerated since usually the entire sample of fingerlings, but often a subsample of fry, was measured.

Sockeye salmon fingerlings (primarily age I) ranged in length from approximately 45 to 118 mm. Many presumably originated in the upper lakes of the Wood River system and had been in Lake Aleknagik by early summer as smolts to migrate out of the lake system. Catches were significantly higher toward the lake outlet (area C) than elsewhere (Tables 3 and 4).

Sockeye salmon fry (age 0) ranged in length from approximately 25 to 60 mm. The length frequencies are symmetric and may be modeled

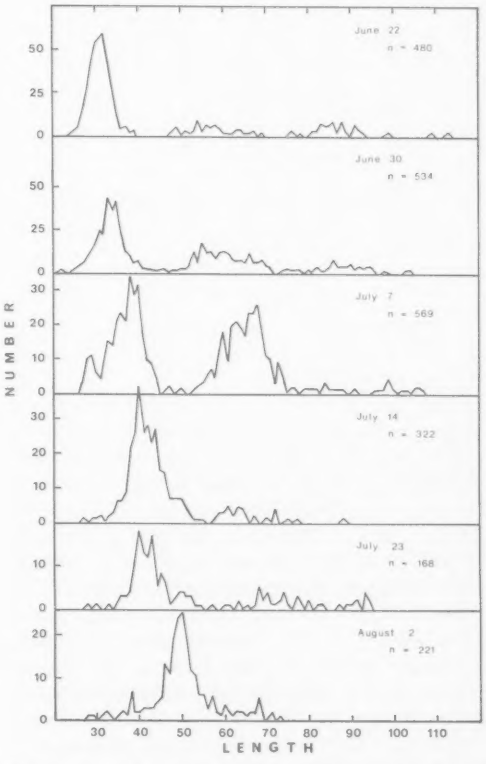

FIGURE 4.—Length-frequency distributions (mm) of sockeye salmon, 1968.

TABLE 3.—Geometric mean beach seine catches in Lake Aleknagik by area and year for the period 20 June-19 July 1962, 1964 through 1972.

Year	Area	*n*	Sockeye fry	Sockeye fingerling	Threespine stickleback	Ninespine stickleback	Sculpin	Char fry
1962	A	12	510.1	4.4	318.5	23.8	52.2	18.3
	B	12	384.8	0.2	301.5	6.2	28.1	4.1
	C	16	109.2	9.4	113.4	12.0	38.2	1.9
	Mean		277.8	3.1	221.7	12.1	38.3	5.6
1964	A	12	140.4	0.0	92.2	7.9	58.3	25.5
	B	12	294.3	0.9	497.2	22.3	52.3	2.1
	C	16	121.9	15.0	463.1	47.8	29.3	0.7
	Mean		171.4	2.1	276.9	20.3	44.7	4.2
1965	A	12	806.3	0.2	102.3	4.2	44.8	9.0
	B	12	1,137.0	1.6	593.8	10.7	25.5	0.9
	C	16	196.6	1.5	130.1	10.6	25.6	0.6
	Mean		564.9	1.0	199.2	7.8	30.8	2.1
1966	A	12	560.2	1.3	127.0	1.5	26.3	24.9
	B	12	446.3	3.0	705.8	5.9	13.3	4.0
	C	16	219.5	4.2	131.8	5.9	16.5	2.0
	Mean		380.0	2.6	227.8	3.7	17.9	6.3
1967	A	12	949.7	3.1	274.0	17.0	51.4	34.9
	B	12	273.7	13.0	737.1	21.6	10.8	3.0
	C	16	145.0	22.8	249.6	27.4	11.5	1.2
	Mean		335.3	10.1	369.4	21.6	18.6	5.8
1968	A	12	44.2	6.3	335.0	33.2	46.5	22.2
	B	12	17.0	4.2	151.8	12.0	17.9	2.4
	C	16	54.6	9.1	142.4	80.1	17.3	2.2
	Mean		34.5	6.3	193.5	31.7	24.3	5.3
1969	A	12	91.9	1.0	208.1	9.0	40.6	6.4
	B	12	106.9	1.9	309.2	15.6	15.8	0.3
	C	15	62.4	2.6	149.2	80.2	28.3	0.8
	Mean		84.9	1.8	212.5	22.4	26.3	1.6
1970	A	12	170.3	0.0	154.7	11.7	24.1	13.9
	B	12	100.9	1.0	95.0	9.6	30.5	2.0
	C	16	120.5	13.7	158.0	37.3	33.5	2.6
	Mean		127.5	2.1	132.4	16.1	29.1	4.4
1971	A	12	404.2	1.1	64.8	5.5	59.8	3.6
	B	12	792.1	4.0	333.8	11.8	35.6	1.3
	C	16	207.9	14.9	378.9	18.2	29.7	0.9
	Mean		405.3	4.5	201.6	10.6	39.8	1.7
1972	A	12	147.6	0.9	18.1	1.4	44.6	14.2
	B	12	721.1	2.5	94.4	4.1	47.4	2.7
	C	16	21.0	3.5	36.9	4.0	17.9	1.1
	Mean		130.7	2.1	39.8	2.8	33.6	3.5

by the normal distribution; however the variability in length in area C was more than in the other areas. This part of the lake tends to warm up earlier in the spring and has a lower abundance of fry. Mean lengths were calculated for 20 June and 20 July from the regression parameters in Table 5. These lengths represent the sizes of fish at the beginning and end of early summer, when sockeye salmon fry were abundant inshore. The fry were of similar length in the lake areas on 20 June, but had become larger in area C than in the others by 20 July (Table 6).

Sockeye salmon fry were more abundant in areas A and B than in area C, apparently because the major spawning ground, Agulowak River, is located here. They were more abundant at the stations adjacent to spawning grounds than at those stations located elsewhere. Most spawning occurs from early August to mid-September. The fry emerge from the gravel from late winter to early spring, and most are in the lake by early June.

Regressions in ln mean catch on coded date (23 June = 1, 1 July = 9, etc.) were calculated for the entire period of sampling (20 June-5 August) and for all periods except the first period (Table 7). The latter results appeared to have greater consistency than the former and indicated that fish were perhaps less available in early spring than later. Catches of sockeye salmon fry declined at a greater rate than

TABLE 4.—Geometric mean beach seine catches in Lake Aleknagik by area and year for the period 21 July-5 August, 1962 through 1972.

Year	Area	*n*	Sockeye fry	Sockeye fingerling	Threespine stickleback	Ninespine stickleback	Sculpin	Char fry
1962	A	6	12.9	2.1	64.8	5.4	26.0	9.2
	B	6	16.4	2.1	58.9	7.7	9.2	9.4
	C	8	3.2	0.0	17.2	2.4	4.5	1.6
	Mean		9.1	1.1	40.6	5.7	10.5	5.5
1963	A	6	0.3	0.4	16.5	4.9	26.7	11.9
	B	6	6.2	0.4	18.2	7.9	2.8	6.5
	C	8	6.5	1.6	40.8	1.2	4.2	7.8
	Mean		3.1	0.7	23.1	3.9	7.2	8.5
1964	A	6	25.3	0.9	395.8	26.6	20.5	21.2
	B	6	41.7	4.2	297.0	12.9	10.4	2.3
	C	8	11.2	0.3	64.6	12.9	9.7	3.4
	Mean		22.9	0.9	197.0	16.5	12.8	5.9
1965	A	3	3,476.8	4.0	756.5	13.5	16.1	15.7
	B	3	15.1	0.4	53.4	4.1	8.5	2.0
	C	4	9.0	0.0	187.8	13.2	11.0	3.2
	Mean		81.4	0.9	197.2	9.2	11.5	4.9
1966	A	6	7.4	0.3	101.4	5.6	9.7	2.1
	B	6	35.0	2.3	249.7	3.8	2.8	1.3
	C	8	26.7	6.1	175.2	7.5	15.2	0.5
	Mean		19.3	2.1	164.4	5.5	7.7	1.2
1967	A	9	127.2	9.9	337.6	15.4	20.0	14.7
	B	9	22.9	8.9	104.3	4.5	3.5	1.5
	C	12	62.2	10.5	100.5	33.3	9.3	0.4
	Mean		56.9	9.7	152.5	13.6	8.9	2.8
1968	A	6	6.1	0.4	167.7	47.5	20.5	0.7
	B	6	3.9	1.7	38.2	17.8	8.4	0.4
	C	8	7.6	1.2	81.0	99.0	14.2	0.0
	Mean		5.7	1.0	80.5	44.0	13.5	0.3
1969	A	6	28.0	0.6	370.4	36.8	39.6	10.2
	B	6	6.9	2.0	46.3	7.0	3.6	1.8
	C	8	26.9	0.7	111.7	46.8	7.9	1.1
	Mean		17.6	1.0	124.6	23.4	10.8	3.0
1970	A	6	46.7	0.0	166.7	16.4	7.0	8.3
	B	6	40.5	3.5	89.7	10.0	16.4	4.5
	C	8	62.3	1.0	221.3	37.4	13.8	3.0
	Mean		49.0	1.1	149.1	18.4	11.7	4.9
1971	A	6	102.3	0.0	43.3	8.6	57.4	4.0
	B	6	13.1	0.7	37.7	3.9	16.7	1.7
	C	8	126.8	6.4	198.3	12.3	11.1	2.0
	Mean		56.1	1.3	68.9	7.6	22.2	2.4
1972	A	6	87.1	11.0	39.9	5.1	53.3	9.0
	B	6	182.7	1.1	149.9	7.6	33.7	4.4
	C	8	25.8	11.2	62.2	7.7	26.0	2.2
	Mean		74.3	5.1	71.9	6.7	36.0	4.4

those of the other species caught by beach seining because this species moves offshore to the pelagic region in midsummer.

Threespine Stickleback

Threespine stickleback were of ages 0 to III and perhaps age IV. They ranged in length from 6 to 81 mm. In years of poor growth, the three major age groups had distinctive length frequencies (Figure 5), whereas in years of good growth, age groups II and III overlapped greatly in length distribution (Figure 6). When, also, ice broke up earlier and water temperatures were higher than average, age 0 fish appeared in the catches before mid-July; threespine stickleback spawn in June and July.

Age I threespine stickleback were usually easy to separate from other age groups from their length, especially within a given lake area. The mean lengths of age I threespine stickleback were greater in area C at both the beginning and end of early summer than in the two other areas (Table 6), but growth rates were similar among the three lake areas.

Threespine stickleback were more abundant along the north shore of the lake than the south. This shore is shallower and has more aquatic

TABLE 5.—Parameters from weighted exponential regression of ln, mean length (live equivalent) on coded date, for Lake Aleknagik beach seine sampling 16 June-5 August, 1962, 1964 through 1972.

		Area A		Area B		Area C		Combined	
Species	Year	[1]a	[2]b	a	b	a	b	a	b
Sockeye fry (Age 0)	1962	3.280	0.0070	3.271	0.0073	3.260	0.0094	3.273	0.0073
	1964	3.242	0.0068	3.293	0.0064	3.266	0.0066	3.291	0.0061
	1965	3.178	0.0087	3.353	0.0027	3.251	0.0051	3.234	0.0067
	1966	3.325	0.0033	3.308	0.0039	3.368	0.0026	3.324	0.0035
	1967	3.304	0.0044	3.229	0.0069	3.183	0.0095	3.267	0.0058
	1968	3.216	0.0097	3.291	0.0102	3.200	0.0122	3.194	0.0118
	1969	3.322	0.0059	3.213	0.0098	3.262	0.0095	3.255	0.0083
	1970	3.221	0.0093	3.236	0.0085	3.135	0.0125	3.192	0.0101
	1971	3.311	0.0040	3.369	0.0019	3.229	0.0069	3.298	0.0043
	1972	3.234	0.0062	3.288	0.0044	3.053	0.0103	3.225	0.0062
	Mean	3.263	0.0065	3.285	0.0062	3.221	0.0085	3.255	0.0070
Threespine stickleback (Age I)	1962	3.252	0.0055	3.218	0.0062	3.374	0.0040	3.269	0.0051
	1964	3.347	0.0033	3.360	0.0035	3.401	0.0029	3.392	0.0027
	1965	3.166	0.0059	3.305	0.0023	3.257	0.0048	3.256	0.0041
	1966	3.187	0.0044	3.232	0.0037	3.181	0.0053	3.215	0.0042
	1967	3.143	0.0059	3.238	0.0046	3.265	0.0057	3.262	0.0038
	1968	3.310	0.0050	3.259	0.0060	3.286	0.0075	3.302	0.0053
	1969	3.304	0.0050	3.448	0.0022	3.335	0.0056	3.399	0.0033
	1970	3.331	0.0053	3.274	0.0062	3.402	0.0050	3.344	0.0051
	1971	3.195	0.0061	3.436	0.0001	3.220	0.0064	3.268	0.0046
	1972	3.095	0.0081	3.209	0.0055	3.383	0.0024	3.216	0.0055
	Mean	3.233	0.0054	3.298	0.0040	3.310	0.0050	3.292	0.0044
Arctic char fry (Age 0)	1964	3.243	0.0049	3.291	0.0041	3.243	0.0050	3.247.	0.0048
	1965	3.238	0.0054	3.348	0.0013	3.312	0.0029	3.259	0.0047
	1966	3.324	0.0025	3.197	0.0057	3.235	0.0046	3.298	0.0032
	1967	3.216	0.0051	3.209	0.0055	3.260	0.0038	3.216	0.0051
	1968	3.332	0.0038	3.373	0.0042	3.075	0.0113	3.305	0.0048
	1969	3.206	0.0060	2.974	0.0105	3.267	0.0060	3.208	0.0061
	1970	3.266	0.0050	3.127	0.0093	3.231	0.0070	3.215	0.0066
	1971	3.270	0.0036	3.307	0.0031	3.270	0.0033	3.284	0.0033
	1972	3.187	0.0058	3.116	0.0085	3.154	0.0060	3.133	0.0074
	Mean	3.254	0.0047	3.216	0.0058	3.227	0.0055	3.241	0.0051

[1] Natural log of mean length on 31 May.
[2] Instantaneous growth rate in length.

vegetation and a larger area of mud bottom; therefore it provides a more suitable forage and spawning habitat. These fish were distributed in much the same pattern as sockeye salmon fry. The two species have common food and some common behavioral habits during the summer (Rogers, 1968). Age I and II fish usually became pelagic in midsummer, and age 0 and III fish tended to remain inshore by late summer.

Ninespine Stickleback

Ninespine stickleback were age 0 to II and perhaps age III. They ranged in length from 10 to 76 mm (Figure 7). The time of spawning and appearance of age 0 fish in the catches were similar to those of threespine stickleback, but growth was more rapid and ages I and II were not as distinctive from length frequencies.

The distribution of ninespine stickleback shows an even greater correlation with location of vegetation and mud bottom than that of threespine stickleback. At stations 2S and 4S where vegetation is sparse on the bottom, catches were always very low. Ninespine stickleback showed the lowest rate of decline in catches among the associated species (Table 7).

Slimy Sculpin

Sculpin ranged in age from 0 to perhaps V but were mostly age I from observations at Iliamna Lake of the Kvichak River system (Roger, 1971). They ranged in length from 8 to 91 mm (Figure 8). As with the sticklebacks,

TABLE 6.—Calculated mean lengths (live equivalent in mm) for 20 June and 20 July from weighted exponential regressions, 1962 through 1972.

Species	Year	20 June				20 July			
		Area A	Area B	Area C	Combined	Area A	Area B	Area C	Combined
Sockeye fry	1962	30.6	30.5	31.4	30.6	37.7	38.0	41.7	38.1
	1963[1]					39.6	45.5	44.0	44.9
	1964	29.3	30.6	29.9	30.3	35.9	37.0	36.4	36.4
	1965	27.4	30.2	28.6	29.0	35.5	32.7	33.2	35.5
	1966	29.7	29.5	30.6	29.8	32.8	33.2	33.0	33.0
	1967	29.7	29.0	29.2	29.5	34.0	35.7	38.8	35.1
	1968	30.2	32.9	31.3	30.8	40.5	44.7	45.2	43.9
	1969	31.2	30.2	31.6	30.6	37.3	40.6	41.9	39.2
	1970	30.2	30.1	29.6	29.8	39.9	38.9	43.1	40.4
	1971	29.7	30.2	29.0	29.5	33.5	32.0	35.6	33.5
	1972	28.7	29.3	26.0	28.5	34.6	33.4	35.4	34.3
	Mean[2]	29.7	30.3	29.7	29.3	36.2	36.6	38.4	36.9
	S.D.	1.05	1.07	1.68	0.75	2.63	4.05	4.33	3.45
Threespine stickleback (Age I)	1962	28.9	28.3	31.7	29.1	34.1	34.0	35.7	33.9
	1963[1]					36.7	39.3	38.4	36.9
	1964	30.3	30.9	31.8	31.4	33.4	34.3	34.7	34.0
	1965	26.7	28.5	28.6	28.1	31.9	30.5	33.0	31.8
	1966	26.4	27.3	26.8	27.0	30.2	30.5	31.4	30.6
	1967	26.1	27.9	29.4	28.2	31.1	32.1	34.8	31.5
	1968	30.3	29.4	31.1	30.2	35.2	35.2	39.0	35.4
	1969	30.1	32.8	31.4	32.0	34.9	35.1	37.1	35.3
	1970	31.1	29.9	33.2	31.4	36.4	36.0	38.6	36.6
	1971	27.6	31.1	28.4	28.8	33.0	31.2	34.4	33.1
	1972	25.9	27.6	30.9	27.8	33.0	32.6	33.1	32.8
	Mean[2]	28.3	29.4	30.3	29.4	33.3	33.2	35.2	33.5
	S.D.	2.01	1.79	1.96	1.74	1.92	2.04	2.46	1.91
Arctic char fry (Age 0)	1963[1]					35.8	36.1	32.1	35.3
	1964	28.2	29.2	28.3	28.3	32.7	33.1	33.0	32.7
	1965	28.4	29.2	29.1	28.6	33.5	30.3	31.7	32.9
	1966	29.2	27.4	27.9	28.9	31.5	32.6	32.0	31.8
	1967	27.6	27.7	28.1	27.6	32.2	32.7	31.6	32.3
	1968	30.2	31.7	27.1	30.0	33.8	36.0	38.0	34.7
	1969	27.8	24.2	29.6	27.9	33.3	33.1	35.4	33.6
	1970	29.0	27.4	29.1	28.4	33.6	36.2	35.9	34.6
	1971	28.2	29.0	28.1	28.5	31.4	31.8	31.0	31.5
	1972	27.2	26.7	26.4	26.6	32.3	34.5	31.6	33.2
	Mean[2]	28.4	28.1	28.2	28.3	32.7	33.4	33.4	33.0
	S.D.	0.92	2.08	1.01	0.93	0.91	1.91	2.47	1.12

[1] Means calculated from lengths on 24 July 1963 and growth rate in 1968.
[2] 1963 excluded.

spawning occurs primarily in June and July, and the entire lifespan is spent in Lake Aleknagik.

Sculpin were the most uniformly distributed of the fish commonly caught by beach seine, but they tended to be more abundant at stations where sockeye salmon spawning occurred (Stations 2N, 5S, 6N, and 7S) than at other stations. Roger (1971) discusses the role of sculpins as predators on sockeye salmon eggs in Lake Iliamna of the Kvichak River system.

Arctic Char Fry

Arctic char spawn in late fall. They are presumably in the lake by early June, although little is known of their reproduction and early life history in Lake Aleknagik. In early summer they are in the fry stage and range in length from 25 to 50 mm. The adults are major predators of juvenile sockeye salmon and threespine stickleback (Nelson, 1966).

Char fry averaged about 1 mm shorter than sockeye salmon fry on 20 June and about 4 mm shorter on 20 July. They did not differ significantly in average length among the lake areas on 20 June, but were smaller in area A than in the other areas on 20 July (Table 6).

Arctic char fry were the most unevenly distributed of the fish caught by beach seine and occurred infrequently in catches. They were more abundant in the upper region of the lake

TABLE 7.—Regression parameters for ln mean catch on coded date (23 June = 1), 1962, 1964 through 1972.

Year	Sockeye fry		Threespine stickleback Age I		Threespine stickleback Age II+		Ninespine stickleback[1]		Sculpin[1]		Char fry[2]	
20 June-5 August	[3]a	[3]b	a	b	a	b	a	b	a	b	a	b
1962	6.600	-0.1092	5.272	-0.0645	4.964	-0.0486	2.122	0.0009	4.188	-0.0472	2.294	0.0135
1964	5.924	-0.0786	5.364	-0.0191	4.844	-0.0175	3.176	-0.0105	4.353	-0.0526	3.022	0.0073
1965	6.104	-0.0239	4.173	0.0158	3.714	0.0344	2.226	-0.0057	3.748	-0.0286	1.582	0.0278
1966	7.040	-0.1012	4.548	-0.0157	4.766	0.0003	1.628	-0.0075	3.203	-0.0274	3.913	-0.0729
1967	6.392	-0.0605	5.397	-0.0454	5.169	-0.0116	2.904	-0.0102	3.250	-0.0305	3.159	-0.0055
1968	4.358	-0.0704	5.504	-0.0771	4.567	-0.0332	3.704	-0.0170	3.815	-0.0541	4.143	-0.1164
1969	4.933	-0.0507	5.106	-0.0131	3.750	-0.0024	3.365	-0.0094	3.582	-0.0311	1.695	0.0143
1970	5.679	-0.0580	3.786	0.0013	4.333	0.0057	2.894	0.0001	3.719	-0.0314	3.062	-0.0322
1971	6.722	-0.0686	4.578	-0.0208	4.633	-0.0081	2.121	0.0085	3.842	-0.0193	1.336	-0.0036
1972	5.081	-0.0275	2.687	-0.0106	3.041	0.0252	0.399	0.0456	3.343	0.0069	2.403	0.0042
Mean	5.383	-0.0649	4.642	-0.0249	4.378	-0.0056	2.454	-0.0005	3.704	-0.0353	2.661	-0.0164
30 June-5 August												
1962	7.226	-0.1299	6.007	-0.0888	5.407	-0.0632	2.721	-0.0182	4.351	-0.0524	4.206	-0.0475
1964	5.807	-0.0745	5.502	-0.0238	4.265	0.0023	3.325	-0.0156	4.248	-0.0491	3.148	0.0030
1965	7.635	-0.0783	5.050	-0.0159	4.310	0.0127	2.203	-0.0049	3.772	-0.0294	1.993	0.0138
1966	7.477	-0.1157	5.747	-0.0551	4.810	-0.0011	1.417	-0.0005	3.128	-0.0250	4.566	-0.0944
1967	6.365	-0.0597	6.666	-0.0848	6.266	-0.0458	3.705	-0.0352	3.739	-0.0457	3.837	-0.0267
1968	4.152	-0.0633	5.713	-0.0842	5.025	-0.0489	4.355	-0.0393	3.671	-0.0492	4.472	-0.1276
1969	5.187	-0.0589	5.774	-0.0346	4.254	-0.0187	3.644	-0.0184	3.781	-0.0376	1.333	-0.0260
1970	6.035	-0.0705	4.667	-0.0296	5.036	-0.0189	2.932	-0.0012	3.970	-0.0398	3.493	-0.0466
1971	7.163	-0.0834	5.338	-0.0463	5.308	-0.0306	2.655	-0.0093	4.061	-0.0265	2.143	-0.0304
1972	5.983	-0.0580	3.201	-0.0280	3.537	0.0085	0.832	0.0310	3.640	-0.0031	3.261	-0.0248
Mean	6.303	-0.0792	5.367	-0.0491	4.892	-0.0106	2.779	-0.0112	3.836	-0.0358	3.245	-0.0355

[1]Calculated from geometric mean catches except age 0.
[2]Calculated from geometric mean catches in lake area A only.
[3]The regression parameter a is the natural logarithm of the calculated catch on 22 June, and the parameter b is the instantaneous rate of decline in catch.

(area A) than in the middle section and the outlet with the exception of station 7S. They were never caught at station 8N. Their distribution in early summer probably reflected the distribution of parent spawners in the previous fall.

Catches of char fry tended to increase during the first four periods of sampling and then to decrease in the last two periods. They may not have been as available to the beach seine as early in the spring as sockeye salmon fry because of later emergence from the spawning grounds.

Annual Variation in Abundance

The geometric mean of the annual mean catches in each area during 20 June-19 July was considered the best estimate of the relative abundance in Lake Aleknagik during the period of the summer when sockeye salmon fry were concentrated inshore. On the average, juvenile sockeye salmon were the most abundant species in the littoral and also exhibited the greatest annual absolute as well as relative variation (coefficient of variation) over the years. Significant differences were detected in the mean catches by year for all species, but the relative annual variations in catches for the next two most abundant species (threespine stickleback and slimy sculpin) were low compared to that of juvenile sockeye salmon.

Linear correlation coefficients were calculated for the purpose of examining relationships among annual estimates of abundance, apparent mortality rates, and selected physical parameters. A total of 84 pairs of variables was examined for correlation and statistically significant correlations at the 5% level were found among 38 pairs. Obviously some caution is needed in the biological interpretation of these data. It is expected that 5% of the tests would reject the null hypothesis that they are independent. Some partial correlation coefficients were examined; however, none were found statistically significant. The notable results of the correlation analysis were: (1) significant positive correlations between water temperature and apparent mortality rate for threespine

stickleback (age I), ninespine stickleback, and sculpin ($n = 10, r = 0.80, 0.84,$ and 0.76, respectively); (2) significant correlation between apparent mortality rates of ninespine stickleback and sculpin ($r = 0.86$); and (3) lack of significant correlations involving sockeye salmon fry. The correlations between water temperature and apparent mortality rate suggest that ninespine stickleback and sculpin populations (which do not become pelagic) experience higher mortality rates at higher water temperatures. The higher mortality may be the result of increased spawning rate and/or rate of predation. Since sockeye salmon fry constitute a major portion of the inshore fish community and exhibit greater annual variation in abundance than the rest,

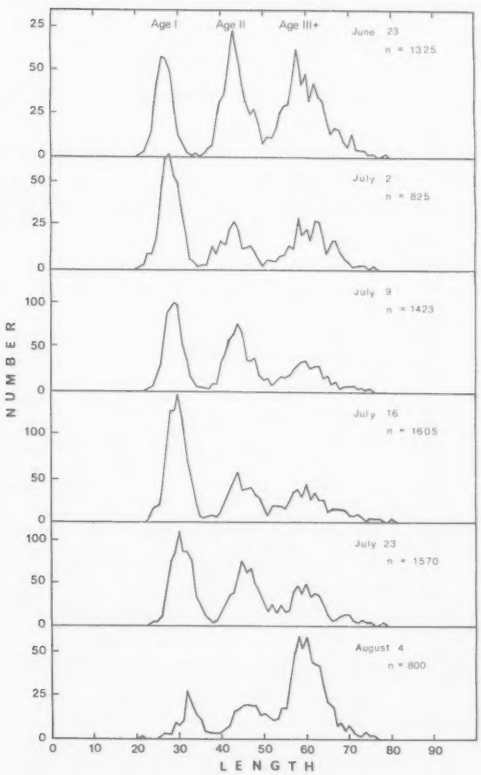

FIGURE 5.—Length-frequency distributions (mm) of threespine stickleback, 1966.

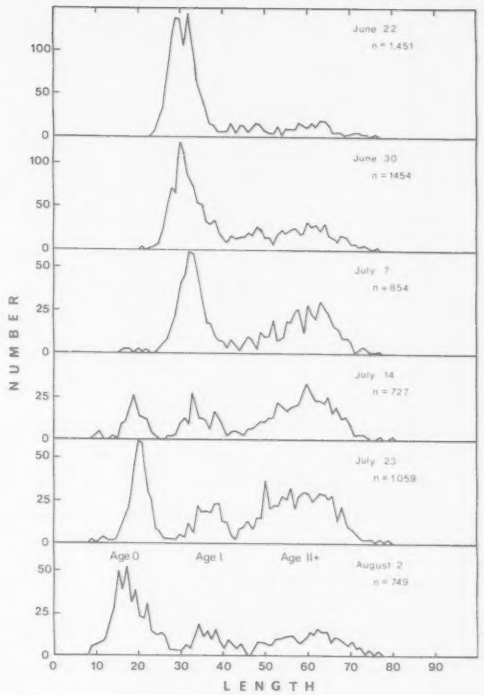

FIGURE 6.—Length-frequency distributions (mm) of threespine stickleback, 1968.

they would appear to have the greatest potential for affecting the abundance of fish of other species. The depressing effect of high abundance of sockeye salmon fry on the abundance of other species was suggested by Parr (1972), but such an effect may be observable only after a time lapse and would be detectable only with observations from a greater number of years. No significant correlation was detected between the catches of sockeye salmon fry and the catches of other species in the same year or in the following year.

A significant, although highly variable, relationship was apparent between the abundance of parent spawners and mean catch of sockeye salmon fry in Lake Aleknagik ($r = 0.62$, $n = 11$). A comparison of the density of sockeye salmon spawners with mean catch of sockeye salmon fry in the Nushagak District is given in Table 8. A positive relation between density of adult

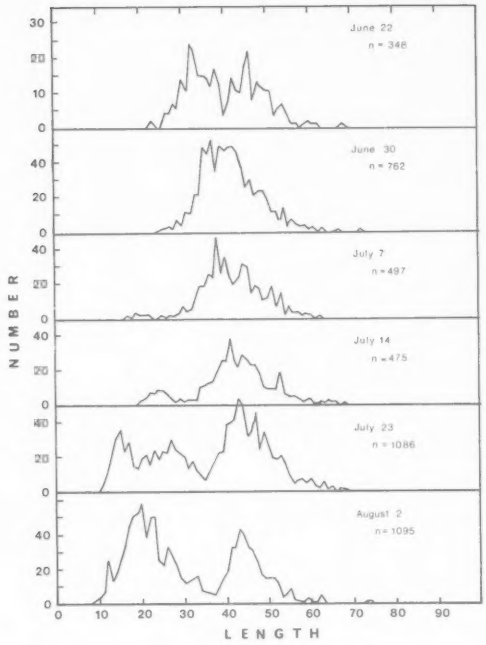

FIGURE 7.—Length-frequency distributions (mm) of ninespine stickleback, 1968.

spawners and density of fry progeny among years and lakes is indicated. The relation between the abundance of fry and the abundance of returning adults is of primary interest because of the possible value in forecasting the magnitude of adult runs. More years of observations are necessary, however, before this relation can be adequately defined.

Annual Variation in Length

Estimates of the average size of the fish in Lake Aleknagik are more precise than estimates of abundance from catches. The annual relative variation in mean length is much less, moreover, than the relative variation in catch. For example, the coefficients of variation in annual mean catches and mean lengths (20 July) for sockeye salmon fry were 67 and 9%, respectively.

The annual estimates of mean length on 20 June and 20 July, which represent the sizes of the fish at the beginning and end of early summer, were examined for determination of the major factors regulating growth. Annual mean lengths of sockeye salmon fry, threespine stickleback (age I), and char fry on 20 June were not significantly correlated. A significant part of the annual variation in lengths of sockeye salmon fry and char fry at this time was explained by the surface water temperatures on 20-24 June (Figure 9). Water temperature on 20 June is largely a function of the date of ice breakup and amount of solar radiation. Thus the annual growth attained in the spring by sockeye salmon fry and char fry is primarily a function of climatological conditions. The mean length of age I threespine stickleback was most closely correlated, however, with the abundance of sockeye salmon fry in the previous year. The best rela-

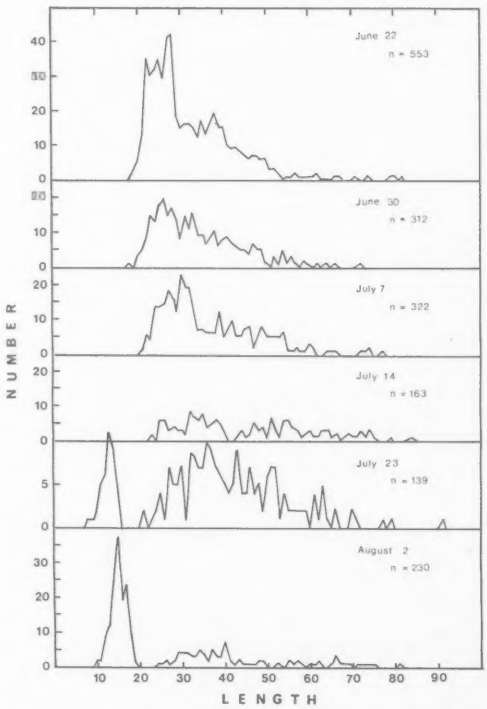

FIGURE 8.—Length-frequency distributions (mm) of slimy sculpin, 1968.

TABLE 8.—Densities of parent spawners and mean beach seine catches of sockeye salmon fry for years and lakes in which six or more seine hauls were made during 20 June-19 July for 1962 through 1972.

Lake	Year (i)	Sockeye salmon escapement in year i-1 (thousands)	Escapement density (number per km² of surface area)	Mean catch of sockeye salmon fry in year i	Adult sockeye salmon returns in years i+3-5 (thousands)
Tikchik lakes	1964	166	595	45	160
Igushik lakes	1965	129	1,743	163	640
Nunavaugaluk	1965	13	146	17	—
	1966	12	135	16	—
Kulik	1969	31	689	36	—
	1970	17	378	50	—
	1971	55	1,222	234	—
	1972	66	1,447	77	—
Beverley	1969	112	1,244	78	—
	1970	27	300	59	—
	1971	238	2,644	71	—
	1972	245	2,722	85	—
Aleknagik	1962	153	1,840	278	497
	1963	48	580	42	203
	1964	31	370	171	321
	1965	155	1,867	565	375
	1966	220	2,646	380	604
	1967	287	3,464	335	262
	1968	92	1,102	34	—
	1969	117	2,129	85	—
	1970	160	1,931	127	—
	1971	302	3,639	405	—
	1972	182	2,193	131	—

tionship was obtained by regressing the mean length on the logarithm of catch (Figure 10). Thus the mean length of threespine stickleback

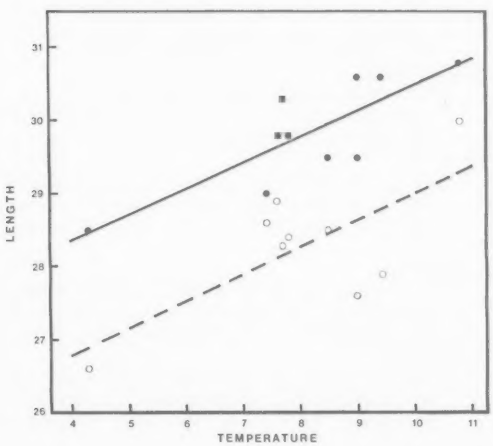

FIGURE 9.—Relationships between mean length (mm) on 20 June and mean surface water temperature from 20 to 24 June. Sockeye salmon fry (0): $Y = 26.93 + 0.36\ X$ ($r = 0.82$). Arctic char fry (0): $Y = 25.31 + 0.37\ X$ ($r = 0.71$).

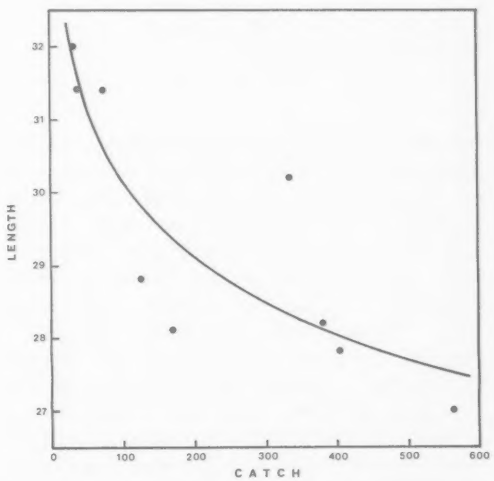

FIGURE 10.—Relationship between mean length (mm) of age I threespine stickleback on 20 June and mean catch of sockeye salmon fry in the previous year (20 June-19 July). $Y = 37.24 - 3.53 \log_{10} X$.

at age I is largely determined by the abundance of their main competitor when they were age 0.

The annual mean lengths on 20 July among

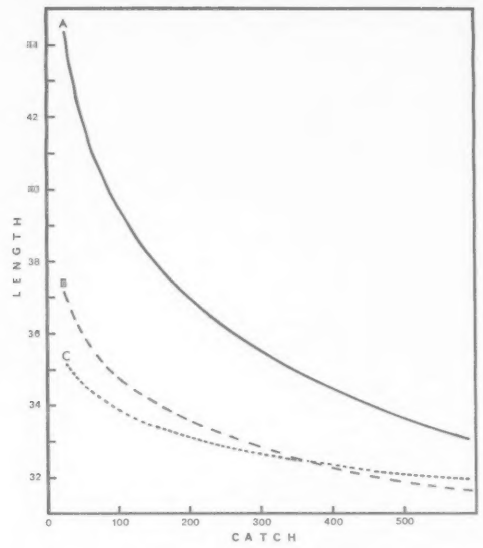

FIGURE 11.—Relationships between mean length on 20 July and mean catch of sockeye salmon fry from 20 June-19 July. A. Sockeye salmon fry: $Y = 56.82 - 8.62 \log_{10} X$ ($r = -0.86$). B. Age I threespine stickleback: $Y = 42.95 - 4.11 \log_{10} X$ ($r = -0.80$). C. Char fry: $Y = 38.93 - 2.56 \log_{10} X$ ($r = -0.85$).

the three species were significantly correlated but were most highly correlated between sockeye salmon fry and char fry ($r = 0.990$). Some correlation was evident between length and (1) date of ice breakup (small size — late date, large size — early date) and (2) average water temperature (small size — cold water, large size — warm water); however the highest correlations were between mean length and the mean catch of sockeye salmon fry. The last relationship appeared to be curvilinear, and regressions of mean length on logarithm of mean catch were significant at the 1% level (Figure 11).

Our main concern is with relationships involving sockeye salmon fry and threespine stickleback, as these are the most abundant species in the littoral. An increasing abundance of sockeye salmon fry results in a decreasing growth of these fish as well as of associated species in early summer. These data suggest a limiting capacity in the lake for growth of individual fish in the populations during the early summer but do not demonstrate a limiting capacity for the number of fish.

Annual variation in the relative abundance of other species did not appear to affect the growth of juvenile sockeye salmon; however, since growth of these species was density dependent (on juvenile sockeye salmon) and these species share a common food supply (primarily aquatic insects), there presumably was competition for food. If larger changes in the abundance of other species occurred in Lake Aleknagik, there would probably be corresponding changes in the growth of juvenile sockeye salmon. This question could best be examined by a comparison of growth and abundance among the lakes of the Wood River system.

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STOMACH CONTENTS OF PORPOISE, *STENELLA* SPP., AND YELLOWFIN TUNA, *THUNNUS ALBACARES*, IN MIXED-SPECIES AGGREGATIONS

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ABSTRACT

Haul-by-haul analysis of stomach contents of spotted porpoise (*Stenella attenuata*), spinner porpoise (*S. longirostris*), and yellowfin tuna (*Thunnus albacares*) from six net hauls made on mixed-species aggregations in 1968 indicates that an ommastrephid squid (probably *Dosidicus gigas*) was the most important food item in terms of co-occurrences in the three species and in terms of the volume and number. The ommastrephid occurred in significant numbers and/or volume in each haul in all the species examined, albeit to a lesser degree in the spinner porpoise than in the other two species. Overlap of elements in the stomach contents was greatest between the tuna and the spotted porpoise. In addition to the ommastrephid, the small scombrid *Auxis* sp. and epipelagic exocoetids such as *Oxyporhamphus micropterus* were important to both. The portunid crab *Euphylax dovii* was very important in the tuna but absent in both species of porpoise. Onychoteuthid and enoploteuthid squids were important in some hauls in both species of porpoise but were all but absent from the tuna. Small mesopelagic fishes, mainly myctophids and gonostomatids, were important in the spinner porpoise, but not in the spotted porpoise or the tuna. Relative frequencies of empty stomachs and state of digestion of stomach contents indicated that the spinner porpoise does not feed at the same time as the spotted porpoise and tuna. In spite of overlap among the three species in nearly all of the food components, these results suggest that the tuna and spotted porpoise feed together largely on epipelagic prey, whereas the spinner porpoise for the most part feeds deeper and at different times of day; furthermore, only the tuna eats crustaceans.

Small pelagic delphinids (*Stenella attenuata*, *S. longirostris*, and *Delphinus delphis*) in the eastern tropical Pacific are commonly encountered with yellowfin tuna (*Thunnus albacares*) in large mixed-species aggregations. The association between the fish and the cetaceans is very tight (Perrin, 1969, 1970). Although the reason for the association is unknown, the possibility that it is food-based immediately suggests itself. Alverson (1963) examined the stomach contents of 2,846 yellowfin tuna from the eastern tropical Pacific and found the major components to be fish (46.9% of total volume) and crustaceans (45.4%). Cephalopods accounted for only 7.6% of the volume. He encountered a wide variety of food items and changes in species composition from area to area. He therefore concluded that yellowfin tuna are nonselective feeders, foraging on whatever pelagic or benthic organisms of suitable size are locally available. Fitch and Brownell (1968) reported on fish identified from otoliths taken from spotted porpoise, *Stenella graffmani* (= *attenuata*)[4] and spinner porpoise (*S. longirostris*) caught in

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[4] The taxonomy of the spotted porpoises is confused. Recent morphological studies (Perrin, 1972) have shown that the spotted porpoise in the eastern Pacific is conspecific with the spotted porpoise that occurs around Hawaii. Accordingly, the name *S. attenuata* (Gray, 1846), which was applied by True (1906) to the Hawaiian form, is used here for the eastern Pacific form. This name has priority by date over *S. graffmani* (Lönnberg, 1934). This usage is provisional, pending the outcome of current studies comparing forms in the Atlantic and Pacific. *S. attenuata* may be a junior synonym of *S. frontalis* (Cuvier, 1829), which was described from the tropical North Atlantic.

TABLE 1.—Collection data for stomach contents examined from yellowfin tuna, spotted porpoise, and spinner porpoise from the eastern tropical Pacific.

Net haul	Date (1968)	Location (lat., long.)	Time of day (h)	Yellowfin tuna captured (t)	Estimated composition of porpoise school			Stomachs examined			
					Stenella attenuata (No.)	*Stenella longirostris* (No.)	*Thunnus albacares* (No.)	*S. attenuata*		*S. longirostris*	
								In field (No.)	In lab (No.)	In field (No.)	In lab (No.)
1	9 April	12°51'N, 93°18'W	1045	6	350	150			32		4
2	12 April	7°11'N, 90°32'W	1245	35	1,300	200	14		25	18	5
3	15 April	7°28'N, 91°15'W	1345	45	300		20	20			
4	16 April	7°30'N, 92°06'W	0800	60	1,500		21	24			
5	17 April	7°50'N, 92°32'W	1100	50	600		19	20			
6	18 April	7°58'N, 92°56'W	1130	35	350	50	5	19		19	
Total							79	83	57	37	9

association with tuna in the eastern tropical Pacific. On the basis of knowledge about the depth distributions of the species encountered, they concluded that the spotted porpoise had been feeding within 30 m of the surface and the spinner porpoise had been feeding to 250 m or more beneath the surface. Squid remains were present in some of the stomachs examined by Fitch and Brownell but were not included in their analysis.

In view of the nonselective feeding habits of the yellowfin tuna, analysis of comparative feeding habits of tuna and porpoise in mixed aggregations must be based on stomach contents collected from two or more of the species taken together in net hauls.

In this paper we report the results of the examination of stomach contents of 79 tuna, 140 spotted porpoise, and 46 spinner porpoise, taken in seine hauls on yellowfin tuna in 1968.

MATERIALS AND METHODS

The animals examined were captured in six net hauls by a tuna seiner (Table 1). The tuna were marked with numbered dart-type spaghetti tags and placed in the vessel's refrigerated fish holds. Stomachs were subsequently collected from the marked fish and preserved entire in 10% Formalin[5] when the catch was unloaded and prepared for processing ashore. Most of the porpoise stomachs were examined in the field and only selected items of the contents preserved in 10% Formalin for later identification (Table 1). The remainder of the stomachs were from animals frozen entire and later dissected ashore. Only the contents of the forestomach (oesophageal stomach) were examined.

The tuna taken during the cruise were nearly all about 1 m long. A random sample of 50 fish ranged from 846 to 1,164 mm fork length (average 1,079 mm).

The entire contents of stomachs opened in the laboratory were rough-sorted into fish, squid, and crustacean components. Each food item was identified to the lowest possible taxon,

[5] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

and the volume was then measured. Whole undigested fish were identified by comparison of external characters with published keys or with identified museum specimens and species descriptions. Usually though, digestion had precluded such a procedure, so the remains were dissected and skeletal features were compared with a large series of radiographs of determined specimens from the collections of Scripps Institution of Oceanography. Fish otoliths extracted from the frozen porpoise stomachs allowed identification of completely and nearly completely digested fish. Because the tuna stomachs were initially preserved in unbuffered Formalin, it was not possible to use otoliths from those stomachs because diagnostic otolith features dissolve rapidly in an acidic solution. Some relatively intact squids (*Dosidicus gigas*, *Symplectoteuthis oualaniensis*, *Abraliopsis affinis*, and *Onykia* sp.) were found and identified in the stomach contents. Beaks from these specimens and from squids taken on the fishing grounds by dipnetting under lights at night were used to identify isolated beaks and beaks associated with otherwise unidentifiable fragments. Published and unpublished keys to cephalopod beaks and beaks from identified squids in the reference collection of the Marine Mammal Division, Northwest Fisheries Center, were also used in the identifications. Beaks from the ommastrephid squids were relatively easy to identify and separate from those of squids of other families. Although a few of the ommastrephids in the stomachs were identifiable to species, the data for the Ommastrephidae in the tables below are subdivided into only three categories: *ommastrephid A* (probably *Dosidicus gigas*), which includes positively identified *D. gigas* and those fragments (with associated beaks) and isolated beaks most probably belonging to that species on the basis of intrafamilial differences in size and darkening of the beaks; *ommastrephid B* (probably *Symplectoteuthis* sp.), which includes positively identified *S. oualaniensis* and those fragments and beaks most probably belonging to that species or another species of *Symplectoteuthis;* and *unidentified ommastrephid*, which includes those fragments and beaks identified only as from ommastrephids. The larger of the two counts of upper and lower beaks was interpreted as the minimum number of individuals represented. The only crustacean identified, *Euphylax dovii*, was present as readily identifiable nearly complete individuals or intact chelipeds. Because many of the porpoise stomachs contained both the remains (otoliths) of very small fish (myctophids, gonostomatids) and of squid, both of which eat small fish and squid, some of the fish and squid identified were almost certainly present only secondarily. The material was analyzed on a haul-by-haul basis, and the data for each haul are presented and discussed separately. Some effect of the nonselective feeding of tuna, the patchy distribution of prey items, may still be present, however. Since the material analyzed includes some stomachs that were full of relatively undigested food and some that contained only squid beaks and/or otoliths from well-digested meals, it is likely that more than one feeding may be represented in the data for some single-net hauls.

The presentation and analyses of the data are patterned after those in the paper by Pinkas, Oliphant, and Iverson (1971), in which both cephalopod beaks and otoliths were used to identify stomach contents of tunas. The analyses are in terms of volume (for the stomachs examined ashore only), numbers, and percent occurrence. Each of these methods distorts the picture in some way. In the numbers and percent occurrence analyses, unimportant small but numerous organisms may be disproportionately evident. The volume analyses are distorting because the various organisms are digested at different rates and because, as mentioned above, some of the contents were freshly ingested while others were only the remnants of well-digested meals. Otoliths and squid beaks tend to be retained in the gut. An ideal method would involve extrapolating an estimate of the original volume of each prey item and calculating caloric content, but these approaches were beyond the scope of the project. The above caveats notwithstanding, the data do yield considerable information on the relative feeding habits of the three species in mixed aggregations.

The stomachs are considered in three categories: full, with traces, and empty. Full stomachs are defined as those containing fleshy re-

TABLE 2.—Stomach contents of spotted and spinner porpoise taken in a single net haul in the eastern tropical Pacific: Haul 1.

	Spotted porpoise, *Stenella attenuata*, 32 stomachs (22 full, 7 with traces, 3 empty)						Spinner porpoise *S. longirostris*, 4 stomachs (all full)					
	Volume		Number		Occurrence		Volume		Number		Occurrence	
Food item	ml	% of total	No.	% of total	No.	% (n = 29)	ml	% of total	total	% of total	No.	% (n = 4)
Total	7,619	100.0	6,101+	100.0	—	—	447	100.0	5,495	100.0	—	—
Fish	246	3.2	272+	4.5+	22	75.9	196	43.9	5,248	95.5	4	100.0
Exocoetidae	202	2.7	43	0.7	15	51.7	0	—	0	—	0	—
Oxyporhamphus micropterus	195	2.6	41	0.7	13	44.8	0	—	0	—	0	—
Exocoetus	7	<0.1	2	<0.1	2	6.9	0	—	0	—	0	—
Myctophidae	32	0.4	204	3.4	18	62.1			3,868	70.4	4	100.0
Diogenichthys sp.	tr.	—	2	<0.1	2	6.9			3,374	61.4	4	100.0
Lampanyctus parvicauda	30	0.4	116	1.9	16	55.2			307	5.6	4	100.0
Lampanyctus idostigma	0	—	0	—	0	—			73	1.1	3	75.0
Benthosema panamense	0	—	0	—	0	—			24	0.4	4	100.0
Myctophum aurolaternatum	tr.	—	6	0.1	5	17.2			25	0.5	3	75.0
Hygophum sp.	0	—	0	—	0	—			5	0.1	4	100.0
Symbolophorus sp.	0	—	0	—	0	—			2	<0.1	1	25.0
Unid. myctophids	2	<0.1	80	1.3	13	44.8			58	1.1	3	75.0
Gonostomatidae:												
Vinciguerria sp.	tr.	—	1	<0.1	1	3.5			98	1.8	3	75.0
Bregmacerotidae:												
Bregmaceros sp.	tr.	—	2	<0.1	2	6.9			842	15.3	4	100.0
Melamphaidae	tr.	—	1	<0.1		3.5			424	7.7	2	50.0
Scopelogadus bispinosus	tr.	—	1	<0.1		3.5			413	7.5	2	50.0
Melamphaes sp.	0	—	0	—	0	—			11	0.2	1	25.0
Stromateidae	tr.	—	8	0.1	5	17.2			0	—	0	—
Cubiceps carinatus	tr.	—	3	<0.1	3	10.3			0	—	0	—
Cubiceps sp.	tr.	—	5	0.1	4	13.8			0	—	0	—
Bathylagidae:												
Bathylagus sp.	0	—	0	—	0	—			11	0.2	1	25.0
Scopelarchidae:												
Unid. scopelarchid	0	—	0	—	0	—			5	0.1	1	25.0
Unid. fish	12	0.2	13+	0.2+	10	34.5	0	—	0	—	0	—
Cephalopods	7,373	96.7	5,820	95.3	29	100.0	245	54.7	247	4.5	4	100.0
Onychoteuthidae:												
Onykia sp.	358	—	3,386	55.5	27	96.6	59	13.1	26	0.5	3	75.0
Ommastrephidae	157	—	1,569	25.8	29	100.0	47	10.4	68	1.2	3	75.0
Ommastrephid A (probably *Dosidicus gigas*)	127	—	1,108	18.2	29	100.0	47	10.4	45	0.8	3	75.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	17	—	216	3.5	27	93.1	0	—	0	—	0	—
Unid. ommastrephid	10	—	257	4.4	12	41.4	tr.	—	23	0.4	1	25.0

196 ml, not identified to species

Enoploteuthidae:													
Abraliopsis affinis	3	—	672	11.0	29	100.0	69	15.3	151	2.7	4	100.0	
Histioteuthidae:													
Unid. histioteuthid	tr.	—	1	0.1	1	3.5	0	—	0	—	0	—	
Chiroteuthidae:													
Unid. chiroteuthid	tr.	—	3	0.1	1	3.5	0	—	2	0.1	1	25.0	
Cranchiidae	tr.	—	3	0.1	2	6.9	0	—	0	—	0	—	
Unid. cranchiid	tr.	—	3	0.1	2	6.9	0	—	0	—	0	—	
Octopoteuthidae:													
Octopoteuthis sp.	tr.	—	1	<0.1	1	3.5	0	—	0	—	0	—	
Unid. cephalopod fragments[1]	16,855	—	—	—	29	100.0	70	15.5	—	—	1	25.0	
Unid. cephalopod beaks	3	—	174	2.9	18	62.1	0	—	0	—	0	—	
Crustaceans	2	—	2	0.1	2	6.9	6	1.3	—	—	1	25.0	
Unid. isopod	2	—	2	0.1	2	6.9	0	—	0	—	0	—	
Unid. gammarid amphipods	0	—	0	—	0	—	6	1.3	—	—	1	25.0	

[1] Includes bulk of fragments of specimens identified from beaks.

mains; stomachs with traces are those containing only squid beaks and fish otoliths and/or skeletal fragments. The volumetric analyses are based on the full stomachs only. The number and occurrence analyses are based on the full stomachs and those with traces. In addition to the material collected from simultaneous catches of two or more of the three predator species, fish otoliths were examined from another 5 spotted porpoise and 14 spinner porpoise captured with yellowfin tuna in various locations in the eastern tropical Pacific (Appendix Tables 1 and 2).

RESULTS

Haul 1

Only the two species of porpoise were sampled in Haul 1 (Table 2). The results for the species are sharply divergent. For the spotted porpoise, cephalopods predominated in volume, numbers, and occurrence. Onychoteuthid, ommastrephid, and enoploteuthid squids were the major food items. Fish made up an insignificant proportion of the volume and consisted primarily of the epipelagic *Oxyporhamphus micropterus*. In the four spinner porpoise examined, squid and fish were present in all the stomachs, each accounting for about half the total volume. The species composition of the squid component of spinner stomachs was different from that in the spotted porpoise mainly in that one of the unidentified ommastrephids (type B, probably *Symplectoteuthis* sp.) was completely absent, whereas it was present in 27 of the 29 spotted porpoise. Fish, primarily myctophids, predominated in numbers, the ratio of fish to squid being almost precisely the reverse of that for the spotted porpoise. Five myctophid species were present in all four stomachs. By far the commonest fish was *Diogenichthys* sp. (probably *laternatus*). A bregmacerotid, *Bregmaceros* sp., was also found in all four stomachs and was the next most common fish, followed closely by the melamphaid *Scopelogadus bispinosus* and the myctophid *Lampanyctus parvicauda*.

Haul 2

All three species were examined in Haul 2 (Table 3). The results for the spotted porpoise

TABLE 3.—Stomach contents of yellowfin tuna, spotted porpoise, and spinner porpoise taken in a single net haul: Haul 2.

Food item	Yellowfin tuna, *Thunnus albacares*, 14 stomachs (12 full, 1 with trace, 1 empty)						Spotted porpoise, *Stenella attenuata*, 25 stomachs (14 full, 8 with traces, 3 empty)						Spinner porpoise, *S. longirostris*, 23 stomachs (5 full, 3 with traces, 15 empty)					
	Volume		Number		Occurrence		Volume		Number		Occurrence		Volume		Number		Occurrence	
	ml	%	No.	% (n = 13)	No.	% (n = 13)	ml	%	No.	%	No.	% (n = 22)	ml (n = 2 full	%	No.	%[1]	No.	%[1]
Total	1,591	100.0	177+	100.0	—	—	762	100.0	1,787	100.0	—	—	1	100.0	439	—	—	—
Fish	844	53.1	34+	19.2	12	92.3	140	18.4	154	8.6	10	45.5		1.8	420	100.0	95.7	2	100.0
Exocoetidae	525	33.0	26	14.7	10	76.9	25	3.3	127	7.1	7	31.8	0	—	0	—	0	—
Oxyporhamphus micropterus	425	26.7	21	11.9	10	76.9	25	3.3	90	5.0	4	18.2	0	—				
Cypselurus sp.	91	5.7	4	2.3	1	7.7	0	—	0	—	0	—	0	—				
Unid. exocoetid	9	0.6	1	0.6	1	7.7	tr.	—	36	2.0	5	22.7	0	—				
Scombridae:																		
Auxis sp.	137	8.6	1	0.6	1	7.7	110	14.4	1	0.1	1	4.6	0	—	0	—	0	—
Myctophidae	0	—	Contents preserved in Formalin; not examined for otoliths				tr.	—	17	1.0	6	27.3	tr.	—	321	73.1	2	100.0
Diogenichthys sp.							tr.	—	3	0.2	3	13.6			37	8.4	2	100.0
Lampanyctus parvicauda							tr.	—	1	0.1	1	4.6			1	0.2	1	50.0
Lampanyctus idostigma							0	—	0	—	0	—			7	1.6	2	100.0
Benthosema panamense							0	—	0	—	0	—			257	58.5	2	100.0
Myctophum aurolaternatum							0	—	0	—	0	—			2	0.5	1	50.0
Myctophum sp.							0	—	0	—	0	—			2	0.5	1	50.0
Symbolophorus sp.							tr.	—	1	0.1	1	4.6			3	0.7	2	100.0
Diaphus sp.							0	—	0	—	0	—			2	0.5	1	50.0
Unid. myctophids							tr.	—	12	0.7	4	18.2			10	2.3	2	100.0
Gonostomatidae:																		
Vinciguerria sp.							0	—	0	—	0				94	21.4	2	100.0
Bregmacerotidae:																		
Bregmaceros sp.							tr.	—	1	0.1	1	4.6			0	—	0	—
Melamphaidae:																		
Scopelogadus bispinosus							tr.	—	1	0.1	1	4.6			0	—	0	—
Stromateidae:																		
Unid. stromateoid							0	—	0	—	0	—			2	0.5	1	50.0
Paralepididae:																		
Unid. paralepidid							0	—	0	—	0	—			1	0.2	1	50.0
Unid. fish	182	11.4	7+	4.0	5	38.5	5	0.7	7	0.4	7	31.8			2	0.5	2	100.0
Cephalopods	363	22.8	131	74.0	13	100.0	622	81.6	1,633	91.4	22	100.0	54	98.2	19	4.3	6	75.0
Onychoteuthidae:																		
Onykia sp.	0	—	0	—	0	—	9	1.2	28	1.6	10	45.5	tr.	—	1	0.2	1	12.5

Ommastrephidae	105	6.6	89	50.3	11	84.6	114	15.0	1,476	82.6	22	100.0	54	—	14	3.2	6	75.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	103	6.5	74	41.8	10	76.9	74	9.7	1,220	68.3	22	100.0	54	—	14	3.2	6	75.0
Ommastrephid B (probably *Symplectoteuthis* sp.	2	0.1	15	8.5	8	61.5	40	5.3	262	14.7	20	90.9	0	—	0	—	0	—
Unid. ommastrephid	0	—	0	—	0	—	tr.	—	6	0.3	1	4.6	0	—	0	—	0	—
Enoploteuthidae:																		
Abraliopsis affinis	0	—	0	—	0	—	1	0.1	109	6.1	16	72.7	tr.	—	1	0.2	1	12.5
Histioteuthidae:																		
Histioteuthis sp.	tr.	—	1	0.6	1	7.7	0	—	0	—	0	—	0	—	0	—	0	—
Unid. octopod	0	—	0	—	0	—	tr.	—	1	0.1	1	4.6	0	—	0	—	0	—
Unid. cephalopod fragments[2]	258	16.2	—	—	5	38.5	498	65.4	—	—	11	50.0	0	—	—	—	0	—
Unid. cephalopod beaks	tr.	—	41	23.2	5	38.5	tr.	—	10	0.6	2	9.1	tr.	—	3	0.7	1	12.5
Crustaceans:																		
Portunidae:																		
Euphylax dovii	373	23.4	12	6.8	7	53.9	0	—	0	—	0	—	0	—	0	—	0	—
Unid. material	11	0.7	—	—	1	7.7	0	—	0	—	0	—	0	—	0	—	0	—

[1] Only two stomachs were examined for otoliths; therefore the sample size for fish numbers and occurrence is two, while that for the cephalopods is eight.
[2] Includes bulk of fragments of specimens identified from beaks.

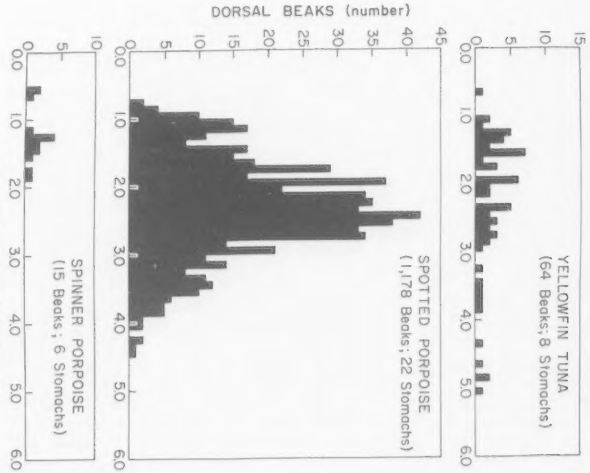

FIGURE 1.—Length frequency distributions of rostral lengths of beaks of ommastrephid squids (type A, probably *Dosidicus gigas*) from stomachs of yellowfin tuna, spotted porpoise, and spinner porpoise taken in a single-net haul (Haul 2) in the eastern tropical Pacific.

were much the same as for Haul 1, especially in that cephalopods strongly dominated in both volume and numbers. In this haul, however, ommastrephids rather than onychoteuthids predominated. Though scanty, the numerical results for the spinner were also similar to those for Haul 1. The relative squid volume was disproportionately large because the fish were represented only by otoliths. The contents of the tuna showed most overlap with those of the spotted porpoise. A scombrid, *Auxis* sp., was present in both. Cephalopods and epipelagic fish were important in both. This overlap, however, was overshadowed by some striking differences. The portunid crab *Euphylax dovii* occurred in half the tuna stomachs and accounted for a fourth of the total volume but was absent from the porpoise stomachs (both species). *Onykia* and enoploteuthid squids each occurred in about half the spotted porpoise stomachs but were absent in the tuna.

TABLE 4.—Stomach contents of yellowfin tuna and spotted porpoise taken in a single net haul: Haul 3.

	Yellowfin tuna, *Thunnus albacares*, 20 stomachs (13 full, 3 with traces, 4 empty)						Spotted Porpoise, *Stenella attenuata*, 20 stomachs (none full, 19 with trace, 1 empty)			
	Volume		Number		Occurrence		Number		Occurrence	
Food item	ml	%	No.	%	No.	%	No.	%	No.	%
Total	837	100.0	112	100.0	16	100.0	75	100.0	—	100.0
Fish	379	45.3	12	10.7	6	37.5	0	—	0	—
Exocoetidae	20	2.4	3	2.7	3	18.8				
Exocoetus volitans	18	2.2	1	0.9	1	6.3				
Unid. exocoetid	2	0.2	2	1.8	2	12.5				
Scombridae:										
Auxis sp.	320	38.2	4	3.6	1	6.3				
Unid. fish	39	4.7	2	1.8	2	12.5				
Cephalopods	3	0.4	78	69.6	8	50.0	[1]75	100.0	19	100.0
Ommastrephidae	2	0.2	68	60.7	8	50.0	66	88.0	2	100.0
Ommastrephid A (probably *Dosidicus gigas*)	2	0.2	53	47.3	8	50.0	32	42.7	2	100.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	tr.	—	16	14.3	6	37.5	34	45.3	2	100.0
Enoploteuthidae:										
Abraliopsis affinis	0	—	0	—	0	—	9	12.0	2	100.0
Unid. Octopod	tr.	—	9	8.0	1	6.3	0	—	0	—
Unid. Cephalopod fragments	1	0.1	—	—	5	31.3	—	—	1	50.0
Unid. Cephalopod beaks	tr.	—	1	0.9	1	6.3	—	—	1	50.0
Crustaceans:										
Portunidae:										
Euphylax dovii	455	54.4	22	19.6	10	62.5	0	—	0	—

[1] Specimens were preserved from two stomachs only; therefore the sample size for the cephalopod taxa is two.

A striking difference between the data for tuna and spotted porpoise on one hand and the spinner porpoise on the other involved the relative number of empty stomachs encountered. Only 1 tuna stomach of 14 and 3 spotted porpoise stomachs of 25 were empty, whereas 15 spinner porpoise stomachs of 23 contained no food remains. The chance of this difference occurring by chance due to sampling error, based on chi-square analysis and assuming commonality of tuna and spotted porpoise, is less than 0.001, indicating that in the aggregation fewer spinner porpoise than spotted porpoise and tuna had been recently feeding or that the spinner porpoise had regurgitated their stomach contents during the fishing operation.

The spinner porpoise had eaten smaller squid than had the spotted porpoise and tuna. Clarke (1962) demonstrated that beak size within a species is closely correlated with total body weight. The sample of beaks of ommastrephid A (probably *Dosidicus gigas*) collected from the spinner porpoise clearly belong to a different size distribution than those taken from the spotted porpoise and the tuna (Figure 1), indicating that the spinner porpoise on the average had been feeding on smaller squid.

Haul 3

Only yellowfin tuna and spotted porpoise were examined in Haul 3 (Table 4). The porpoise stomachs were all nearly empty, containing only hard parts of squid. Except for the complete absence of fish in the porpoise stomachs, the results for the two species were similar

TABLE 5.—Stomach contents of yellowfin tuna and spotted porpoise taken in a single net haul: Haul 4.

	Yellowfin tuna, *Thunnus albacares*, 21 stomachs (20 full, 1 empty)						Spotted porpoise, *Stenella attenuata*, 24 stomachs (23 full, 1 with traces)[1]					
	Volume		Number		Occurrence		Volume		Number		Occurrence	
Food item	ml	%	No.	%	No.	%	ml (n=3)	%	No.	%	No.	%
Total	1,411	100.0	139	100.0	20	100.0	653	100.0	—	—	—	—
Fish	108	7.5	10	7.2	5	25.0	2	0.3	6	—	5	21.7
Exocoetidae	54	3.8	4	2.8	4	20.0	1	0.2	4	—	4	17.4
Oxyporhamphus micropterus	24	1.7	2	1.4	2	10.0	—	—	1	—	1	4.4
Exocoetus monocirrhus	0	—	0	—	0	—	1	—	2	—	2	8.7
Exocoetus sp.	29	2.0	1	0.7	1	5.0	—	—	0	—	0	—
Unid. exocoetid	8	0.6	1	0.7	1	—	—	—	1	—	1	4.4
Scombridae:												
Unid. scombrid	0	—	0	—	0	—	—	—	1	—	1	4.4
Unid. fish	54	3.7	6	4.3	2	10.0	tr.	—	2	—	2	8.7
Cephalopods	633	43.9	77	55.4	0	—	652	99.9	85	—	23	100.0
Onychoteuthidae:												
Onykia sp.	0	—	0	—	0	—	tr.	—	4	—	1	4.4
Ommastrephidae	615	42.7	38	27.3	11	55.0	650	99.5	49	—	3	100.0
Ommastrephid A (probably *Dosidicus gigas*)	609	42.3	27	19.4	10	50.0	515	78.9	35	—	3	100.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	6	0.4	11	7.9	4	20.0	135	20.7	14	—	1	33.3
Enoploteuthidae:												
Abraliopsis affinis	0	—	0	—	0	—	tr.	—	31	—	3	100.0
Unid. octopod	tr.	—	1	0.7	1	5.0	0	—	0	—	0	—
Unid. cephalopod fragments	18	1.3	—	—	1	5.0	2	0.3	—	—		33.3
Unid. cephalopod beaks	tr.	—	2	1.4	2	10.0	tr.	—	1	—	1	33.3
Crustaceans:												
Portunidae:												
Euphylax dovii	700	48.6	37	26.6	14	70.0	0	—	0	—	0	—

[1] Complete contents were preserved and volumed for only three stomachs. All fish remains were preserved; therefore the sample size for fish number and occurrence is 23. For cephalopod taxa, the sample size is three.

to those in Haul 2. Overlap was greatest in the cephalopod component. The crab *Euphylax dovii* was dominant in the tuna and absent in the porpoise. The enoploteuthid squid *Abraliopsis affinis* was again present in the porpoise but absent from the tuna. Nearly all of the fish volume in the tuna was due to the presence of four frigate mackerel, *Auxis* sp., in one stomach.

Haul 4

Tuna and spotted porpoise were again sampled in Haul 4 (Table 5), and the same pattern emerged as in the previous hauls. Portunid crabs were important in the tuna but absent in the porpoise, and enoploteuthid squid were present in the porpoise but absent in the tuna. Except for *Abraliopsis*, the squid and fish components were very similar for the two species in this haul.

Haul 5

Both the tuna and the spotted porpoise in this haul were engorged with freshly ingested *Auxis* and squid (Table 6), and the makeup of the contents in both volume and number was remarkably similar. They had obviously fed on the same food at the same time. *Abraliopsis*

TABLE 6.—Stomach contents of yellowfin tuna and spotted porpoise taken in a single net haul: Haul 5.

	Yellowfin tuna, *Thunnus albacares*, 19 stomachs (all full)						Spotted porpoise, *Stenella attenuata*, 20 stomachs (17 full, 2 with traces, 1 empty)			
	Volume		Number		Occurrence		Number		Occurrence	
Food item	ml	%	No.	%	No.	%	No.	%	No.	%
Total	17,411	100.0	222	100.0	19	100.0	194	100.0	19	100.0
Fish	13,019	74.8	110	49.6	19	100.0	[1]97	<50.0	16	84.2
Exocoetidae:										
Oxyporhamphus micropterus	197	1.1	8	3.6	6	31.6	1	<0.5	1	5.3
Exocoetus volitans	107	0.6	5	2.3	4	21.1	1	<0.5	1	5.3
Unid. exocoetid	29	0.2	1	0.5	1	5.3	0	—	0	—
Scombridae:	61	0.4	2	0.9	2	10.5	0	—	0	—
Auxis sp.	12,720	73.1	91	41.0	19	100.0	91	<46.9	15	79.0
Unid. fish	102	0.6	11	5.0	5	26.3	5	<2.6	5	26.3
Cephalopods	4,392	25.2	112	50.5			[2]>97	>50.0	18	94.7
Onychoteuthidae:										
Onykia	0	—	0	—	0	—	present		—	—
Ommastrephidae:										
Ommastrephid A (probably *Dosidicus gigas*)	4,389	25.2	88	39.6	15	79.0	present		—	—
Ommastrephid B. (probably *Symplectoteuthis* sp.)	tr.	—	10	4.5	4	21.1	present		—	—
Enoploteuthidae:										
Abraliopsis affinis	tr.	—	3	1.4	2	10.5	present		—	—
Unid. cephalopod fragments	3	<0.1	—	—	1	5.3	—		—	—
Unid. cephalopod beaks	tr.	—	11	5.0	5	26.3	—			

[1] Fish counted in 19 stomachs.
[2] Whole squid counted in 16 stomachs not saved ; only samples of beaks were saved for identification.

was present in the tuna (beaks from three individuals), the only occurrence in tuna in the six hauls. *Onykia*, however, was again present in the porpoise but not in the tuna.

Some of the frigate mackerel were sufficiently undigested to allow them to be measured. Thirty five ranged from 18 to 29 cm fork length (average 24 cm), and sizes did not differ in porpoise and tuna.

Haul 6

Nineteen stomachs of spinner porpoise were examined in this haul, and all were empty. The spotted porpoise contained freshly ingested *Auxis* and squid (Table 7), in about the same ratio as in Haul 5, but the tuna contained only small amounts of *Euphylax dovii*, along with well-digested fish and squid remains. The three species in this haul had fed on different food and/or at different times.

Summary of Results

Ommastrephid squid A (probably *Dosidicus gigas*) was the most important prey species in terms of co-occurrence in the tuna and both species of porpoise as an important food item (Table 8). The greatest overlap between species was in Haul 5, when *Auxis* and the ommastrephid were important in the tuna and the spotted porpoise. As regards specialization, *Diogenichthys* sp., *Benthosema panamense*, *Vinciguerria* sp., and *Bregmaceros* sp. were important only in the spinner porpoise, and *Euphylax dovii* was important only in the tuna. When spinner porpoise were sampled (three hauls), the rate of occurrence of empty stomachs and the state of

TABLE 7.—Stomach contents of yellowfin tuna, spotted porpoise, and spinner porpoise taken in a single net haul: Haul 6.

Food item	Yellowfin tuna, *Thunnus albacares*, 5 stomachs (4 full, 1 empty)						Spotted porpoise, *Stenella attenuata*, 19 stomachs (12 full, 4 with traces, 3 empty)				Spinner porpoise, *S. longirostris*, 19 stomachs (all empty)
	Volume		Number		Occurrence		Number		Occurrence		
	ml	%	No.	%	No.	%	No.	%	No.	%	
Total	217	100.0	>33	100.0	4	100.0	>113	100.0	16	100.0	
Fish	68	31.3	6	18.1	3	75.0	32	<28.3	9	56.3	
Exocoetidae: *Oxyporthamphus micropterus*	15	6.9	1	3.0	1	25.0	0	—	0	—	
Scombridae: *Auxis* sp.	0	—	—	—	0	—	32	<28.3	9	56.3	
Unidentified fish	53	24.4	5	<15.2	3	75.0	0	—	0	—	
Cephalopods	tr.	—	>8	>24.2	4	100.0	[1]>81	>71.7	16	100.0	
Ommastrephidae	tr.	—	5	<15.2	1	25.0			—	—	
Ommastrephid A (probably *Dosidicus gigas*)											
Unidentified cephalopod beaks	tr.	—	>3	>9.1	3	75.0			—	—	
Crustaceans: Portunidae: *Euphylax dovii*	149	68.7	5	<15.2	2	50.0	> 0	—	0	—	

[1] Whole squid counted in 12 full stomachs, not saved; beaks not counted or saved.

digestion of the stomach contents indicated that they had not fed at the same time as the tuna and/or the spotted porpoise.

DISCUSSION

Interpretation of the feeding habits of animals from their stomach contents is complicated by two factors. First, material from the stomachs of the primary prey may be mistaken as food items of the predator. This is especially true when, as in the present study, many stomachs contain squid, which are active piscivores in their own right. However, if we are concerned only with the general depth at which feeding takes place, it makes less difference whether the fish remains found in the gut are primary or secondary in origin. When two predators show consistent differences in the probable depth origin of their stomach contents, there are at least three alternative interpretations: the two predators feed at different depth ranges (gathering the material found directly or through some secondary predator), they feed at the same depths but at different times of the day, thus taking advantage of diurnal migration of some prey species, or they feed at the same depth with one only eating prey items that were recent predators at another depth. The first explanation seems most probable.

The other complicating factor is less easy to resolve. The depth distributions of many pelagic prey items are imperfectly known. This requires that much caution be exercised when interpreting food habits of predators from data based on rare or little-known prey.

Depth Distribution of Fish

Exocoetidae

Oxyporhamphus micropterus and species of both *Exocoetus* and *Cypselurus* are all constant inhabitants of epipelagic waters. Exocoetids were extremely common in the stomachs of tuna and *S. attenuata*. Only one exocoetid otolith was found in all 46 stomachs of *S. longirostris* examined.

Scombridae

The frigate mackerel, *Auxis* sp., is another common fish of surface waters and is of relatively large size. Its occurrence in specimen stomachs parallels that of the flyingfish, often being found in *S. attenuata* and yellowfin tuna

TABLE 8.—Summary of major identified stomach constituents of yellowfin tuna, spotted porpoise, and spinner porpoise taken from mixed-species aggregations in the eastern tropical Pacific. + = present, ● = important (≥ 10% of volume and/or numbers).

Food item	Haul 1		Haul 2			Haul 3		Haul 4		Haul 5		Haul 6		
	Spotted	Spinner	Tuna	Spotted	Spinner	Tuna	Spotted	Tuna	Spotted	Tuna	Spotted	Tuna	Spotted	Spinner
FISHES:														
Oxyporhamphus micropterus	+		●	+				+	+	+	+	+		
Auxis sp.			+	●		●				●	●		●	
Diogenichthys sp.	+	●	(Otoliths not collected)	+	+	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(all empty)
Benthosema panamense		+			●									
Vinciguerria sp.	+	+			●									
Bregmaceros sp.	+	●		+										
SQUIDS:														
Onykis sp.	●	●		+	+									
Ommastrephid A (probably *Dosidicus gigas*)	●	●	●	●	●	●	●	●	●	●	●	●	(Squids not identified)	
Ommastrephid B (probably *Symplectoteuthis* sp.)	+		+	+		●	●	+	●	+	+			
Abraliopsis affinis	●	●		+	+		●			+	+			
CRAB:														
Euphylax dovii			●			●		●				●		

and completely absent as a food item of *S. longirostris*.

Myctophidae

At least 13 species of myctophids were identified from specimen stomachs. A majority of the genera found (*Diaphus, Diogenichthys, Ceratoscopelus, Hygophum, Myctophum, Symbolophorus, Benthosema*, and *Gonichthys*) are known to reach the surface at night during the course of vertical migrations, but most remain deep during the day. A second group consisting of *Lepidophanes, Lampanyctus, Lobianchia*, and *Triphoturus* are usually not caught in near-surface waters, even at night; their migrations probably do not take them as shallow as the first group. Myctophids were a consistent major food item of *S. longirostris* and occasionally were common in *S. attenuata*.

Gonostomatidae

Vinciguerria is a vertical migrator found below 200 m during the day, ranging up to surface waters at night. Three-fourths of the full stomachs of *S. longirostris* examined for otoliths contained gonostomatid remains. In the much larger sample of spotted porpoise stomachs, only two contained a few gonostomatid otoliths.

Stromateidae

Although some young stromateoids are often associated with floating objects, adults have large depth ranges. *Cubiceps carinatus* has been taken in a midwater trawl station in large numbers. Stromateoids appeared irregularly in the stomachs of both species of porpoise.

Melamphaidae

Melamphaes and *Scopelagadus* adults normally remain below 100 to 200 m) Ebeling, 1962; Ebeling and Weed, 1963). Melamphaid otoliths were found occasionally in large numbers in *S. longirostris* stomachs and rarely (cf. Appendix 1) in those of *S. attenuata*.

Bregmacerotidae

Although *Bregmaceros* is known to occur bathypelagically and is captured in midwater trawls, it also can be found at the surface at night (Fitch and Brownell, 1968). It occurred regularly in low frequencies in both species of porpoises; larger numbers were found in one associated group of four porpoise (*S. longirostris*).

Gempylidae, Trachipteridae

Species of both these families have been found both in surface waters and at depth. A trachipterid otolith was found in the gut of one *S. longirostris*. Gempylid remains were found in two spinner porpoise stomachs, and in one *S. attenuata* from the far-west sampling area (Appendix 1).

Paralepididae, Bathylagidae, Scopelosauridae, Evermannellidae, Opisthoproctidae

Adult members of these families are not normally found near the surface. Most museum specimens have been caught in midwater trawls. A few otoliths from species in these families were regularly found in the stomachs of *S. longirostris*. Two specimens of *S. attenuata* caught in the far-west sampling location (Appendix 1) also contained otoliths from these families, including the only records of scopelosaurids and opisthoproctids. Otoliths from many myctophids and melamphaids were also found in these specimens. The overall pattern closely parallels that seen for spinner porpoise normally (e.g., Appendix 2). This indicates that spotted porpoise are capable of shifting to a mesopelagic feeding pattern, although epipelagic feeding appears to be typical. The cause of the shift is unknown.

Shomura and Hida (1965) reported that the stomach of a Hawaiian spotted porpoise contained fish of the families Paralepididae, Alepisauridae, Gempylidae, Bramidae, and Myctophidae, as well as squids (the major component), nemertean worms, and crab larvae. The fish component was similar to that for the two westernmost specimens of eastern Pacific *S. attenuata* discussed above.

Depth Distributions of Squids

No discrete depth sampling of squids has been carried out in the area where the animals were collected. Some information, however, is available on the depth distributions of some of the families concerned from other areas.

Ommastrephidae

The most abundant squids found in the stomachs were probably *Dosidicus gigas* and *Symplectoteuthis* sp. Clarke (1966) reported that *D. gigas* and species of *Symplectoteuthis* migrate to the surface at night. *Dosidicus gigas* and *Symplectoteuthis oualaniensis* have been taken in the area by dip net at the surface under lights at night (unpublished data). In this area, the ommastrephids are the most abundant epipelagic squids.

Enoploteuthidae

The enoploteuthid squid *Abraliopsis affinis* occurred next in abundance to the ommastrephids. It is a mesopelagic species. Gibbs and Roper (1972) stated that enoploteuthids undergo diurnal vertical migrations. It appears that this species may move into or is resident within the diving ranges of the two species of porpoise,

but does not occur regularly in the possibly more epipelagic range of the tuna. Another possibility, of course, is that it is fed on selectively by the porpoise and not by the tuna.

Onychoteuthidae

Onykia sp. was not found in the stomachs of *Thunnus* and has not been taken by dip net at the surface in the area. However, it was found in the stomachs of the two species of porpoise and may be a mesopelagic species. Other members of the family, *Onychoteuthis* sp. for example, are regularly taken at or near the surface at night.

SUMMARY

While there is great overlap among the diets of the two porpoises and the tuna in mixed aggregations, there is evidence of specialization in prey items, time of day at which feeding occurs, and possibly in maximum feeding depth. Although the three species are intimately associated in tight mixed groups, they do not necessarily feed on the same items at the same time in the same place. If the association is food-based, however, the epipelagic ommastrephid squids seem to be the most probable candidates for a binding common factor in this region. The apparent trophic relationships among the three species can be crudely summarized in terms of taxa and depth distribution of the major prey items (Figure 2).

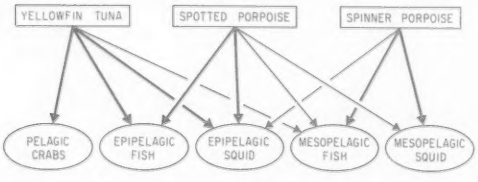

FIGURE 2.—Summary of apparent relative feeding habits of yellowfin tuna, spotted porpoise, and spinner porpoise in mixed aggregations in the eastern tropical Pacific, based on stomach-content data presented here and in Fitch and Brownell (1968) and Alverson (1963). Widths of lines crudely approximate relative importances of the major food categories.

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APPENDIX TABLE 1.—Fish identified from otoliths taken from stomachs of five spotted porpoise, *Stenella attenuata*, caught with yellowfin tuna in the eastern tropical Pacific. When more than one stomach in sample, frequency of occurrence given in parentheses. Data supplement those in Tables 2-7.

Fish	Locality 1 7°47'N 106°50'W 18 April 1969 (1 stomach)	Locality 2 7°-8°N 106°-107°W 27-28 April 1969 (1 stomach)	Locality 3 4°-7°N 86°-100°W June-July 1970 (1 stomach)	Locality 4 9°28'N 129°18'W 12 Aug. 1970 (2 stomachs)
	(minimum number of individuals)			
Exocoetidae:				
Cypselurus sp.			2	
Exocoetus sp.			1	9(2)
Oxyporhamphus sp.				2(2)
Unid. exocoetid(s)	2	3		
Myctophidae:				
Diaphus spp.				34(2)
Diogenichthys laternatus				62(2)
Hygophum spp.				4(2)
Lampanyctus spp.				340(2)
Lepidophanes sp.				12(2)
Myctophum spp.				6(2)
Symbolophorus sp.				26(2)
Unid. myctophids	6		1	76(2)
Melamphaidae:				
Melamphaes spp.				18(2)
Scopelogadus sp.				29(2)
Gonostomatidae:				
Unid. gonostomatid				4(1)
Stromateidae:				
Cubiceps carinatus				9(2)
Cubiceps sp.			1	
Unid. stromateoids				5(2)
Gempylidae:				
Unid. gempylid				3(1)
Paralepididae:				
Unid. paralepidid				3(2)
Bathylagidae:				
Bathylagus sp.				23(2)
Bregmacerotidae:				
Bregmaceros sp.				2(2)
Scopelosauridae:				
Scopelosaurus sp.				1
Opisthoproctidae:				
Dolichopteryx sp.				1
Evermannellidae:				
Evermannella sp.				2(1)
Total	8	3	5	671

APPENDIX TABLE 2.—Fish identified from stomachs of 14 spinner porpoise *Stenella longirostris*, caught with yellowfin tuna in the eastern tropical Pacific. When more than one stomach in sample, frequency of occurrence given in parentheses. Data supplement those in Tables 2-7.

Fish	Locality					
	1	2	3	4	5	6
	7°-8°N 106°-107°W 26-27 Apr. 1969 (4 stomachs)	7°-8°N 107°W 28 Apr. 1969 (2 stomachs)	3°-10°N 110°-120°W June 1970 (1 stomach)	10°19'N 135°38'W 5 Aug. 1970 (1 stomach)	9°47'N 133°25'W 11 Aug. 1970 (5 stomachs)	9°10°N 128°-136°W Aug. 1970 (1 stomach)
Exocoetidae:						
Oxyporhamphus micropterus	1					
Myctophidae:						
Ceratoscopelus sp.	6(1)		1			1
Diaphus spp.	102(3)	3(2)	57	1	191(5)	58
Diogenichthys laternatus			624	5	3,347(5)	398
Diogenichthys sp.	8,732(3)	109(1)				
Hygophym spp.	100(1)	3(1)	4		60(5)	7
Lampanyctus parvicauda	8(3)	2(2)				
Lampanyctus idostigma	111(2)	10(1)				
Lampanyctus spp.			613	163	2,369(5)	899
Lepidophanes sp.			14		131(4)	15
Lobianchia dofleini			239		582(5)	236
Myctophum aurolaternatum	195(2)	1				
Myctophum spp.					10(3)	
Symbolophorus sp.	17(2)		12	1	38(5)	9
Benthosema panamense	68(2)	12(2)				
Gonichthys tenuiculum	79(2)					
Triphoturus sp.	3(1)					
Unid. myctophids	115(4)	29(1)			179(4)	8
Melamphaidae:						
Melamphaes spp.	6(1)	1	2		42(2)	
Scopelogadus bispinosus	1	2(1)		49		
Gonostomatidae:						
Vinciguerria sp.	32(2)	4(1)	50		55(5)	42
Unid. gonostomatids			2		52(2)	1
Stromateidae:						
Cubiceps carinatus	10(1)	1	1	6	2(2)	4
Cubiceps sp.					2(1)	
Unid. stromateoids	3(2)		3		3(2)	2
Gempylidae:						
Unid. gempylid				2	1	
Paralepididae:						
Unid. paralepidid			2			
Bathylagidae:						
Bathylagus sp.	22(1)		11		2(1)	5
Bregmacerotidae:						
Bregmaceros sp.	1		2		9(4)	1
Evermannellidae:						
Evermannella sp.	5(1)		1		2(2)	
Stomaitidae:						
Unid. stomiatoids	1		1			
Trachipteridae:						
Trachipterus fukuzakii	1					
Total	9,619	177	1,639	227	7,167	1,686

SEA GRASSES AT KHOR UMAIRA, PEOPLE'S DEMOCRATIC REPUBLIC OF YEMEN WITH REFERENCE TO THEIR ROLE IN THE DIET OF THE GREEN TURTLE, *CHELONIA MYDAS*

HAROLD F. HIRTH, LIONEL G. KLIKOFF, AND K. T. HARPER[1,2]

ABSTRACT

Studies were made on the sea grass pastures at Khor Umaira in the People's Democratic Republic of Yemen in July 1972. The standing crop in an equally mixed pasture of *Cymodocea serrulata* and *Syringodium isoetifolium* was greater than that in a pure stand of *C. serrulata*. The average caloric content of the leaves of five genera of sea grasses at Khor Umaira ranged between 4.54 and 4.66 kcal/g dry wt, ash free. These values are similar to those reported for sea grasses in the South Pacific and in the Caribbean. Our results show that the number of calories in the standing crop can be calculated from estimation of percent cover. The role of sea grasses in the management schemes of the green turtle, *Chelonia mydas*, is described.

Sea grass meadows are productive and important marine communities. Besides stabilizing the substrate sea grasses provide cover and are a source of food for a number of marine invertebrates and vertebrates. The leaves also support a variety of epiphytes and the grass debris serves as the energy base for detritus food chains. It is probable that in earlier days large numbers of manatees, dugongs, and green turtles grazed on these submarine pastures, but the sirenians and marine turtles have been so over-exploited that today many marine meadows are virtually ungrazed by any big vertebrate of economic importance to man. The green turtle, *Chelonia mydas*, has been proposed as a candidate for marine ranching by fencing them in underwater spermatophyte pastures (for review of management schemes see Hirth, 1971). The purposes of this paper are to describe some basic parameters of the sea grass pastures at Khor Umaira in the People's Democratic Republic of Yemen and to provide basic data aimed at answering the question, "What are the characteristics of good green turtle feeding pastures?" Khor Umaira has been mentioned as a possible site for a green turtle ranch (Food and Agriculture Organization, 1968).

THE SITE

Khor Umaira is the name of a bay (an arm of the Gulf of Aden) and village approximately 80 km west of Aden. The bay is almost completely landlocked by a long, narrow sandy spit that extends west-northwest along the coast. The bay itself is about 6.5 km long. Its width varies from about 550 m at the entrance to approximately 3.2 km in the middle. The depth of the water near the entrance is between 1 and 6 m, while the depth inside varies from 1 to 11 m.

Quantitative data were taken inside the bay where a few green turtles are always seen feeding. The grass pasture in the bay was adjudged similar to that off the nearby coast at comparable depths where large numbers of grazing turtles are caught in seines.

METHODS

Five adult female green turtles, all weighing over 91 kg, were caught on the Ras al Ara pastures (19 km west of Khor Umaira) on 22 July 1972. Their stomachs were full of leaves of sea grasses (chiefly *Syringodium* and *Cymodocea*) along with some stems and a few segments of

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rhizomes (see Figure 1). Observations made in 1966-67 (Food and Agriculture Organization, 1968) also suggest that green turtles in the vicinity of Khor Umaira eat chiefly the leaves of sea grasses. The local name for all sea grasses is Zawee.

No turtles were observed grazing in the census plots at the time of collection, but substantial amounts of leaves had washed up on the shores of the bay.

The grasses were collected in the middle of what was considered good turtle pasturage on 28, 29, and 30 July 1972. This was during the peak of the Southwest Monsoon which in this area generally prevails from April through September. The collecting sites were approximately 500 to 600 m from the nearest shore. Thirty samples were taken in a homogeneous pasture of *Cymodocea serrulata* and 30 samples from a stand of *C. serrulata* and *Syringodium isoetifolium* adjudged to be equally mixed. The sample quadrats were 1/16 m^2. The 60 samples were taken at depths from 0.8 to 2.5 m with 70% of the samples from depths of 1.8 to 2.5 m. The sampling was done at or near low tide. Visibility, as measured with a white Secchi disc 20 cm in diameter, extended to the bottom. Pure stands of *Syringodium* were not seen in the bay but a more detailed census might reveal the presence of such stands.

The grasses were harvested at the ground surface and weighed. No attempt was made to separate epiphytic algae from the leaves. Wet weight was obtained after removing the external water by gentle blotting and dry weight was determined by drying to constant weight in an oven at 80°C. Cover was calculated by looking straight down on a 1/16 m^2 quadrat and estimating percent coverage to the nearest 10%. Caloric values were determined using a Parr semimicro bomb calorimeter[3] following the procedures of Lieth (1968). However, since some of the techniques with oxygen bomb combustion underestimate ash content (Paine, 1971; Reiners and Reiners, 1972) in a second series of combustions aliquots of the material were ashed at 500°C for 5 h in a muffle furnace for determination of ash content. All caloric determinations are means of three samples and each sample differed by less than 3%. Plant nomenclature and terminology follows den Hartog (1970). Regression procedures follow those given in Steel and Torrie (1960).

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

FIGURE 1.—The stomach contents of an adult, female green turtle caught on 22 July 1972 on the feeding pasture near Ras al Ara. The stomach was packed solidly with sea grasses.

RESULTS AND DISCUSSION

The dry weights of *C. serrulata* along with corresponding cover data are given in Figure 2. All of the leaf blades on the sample plots were less than 20 cm long, with shorter blades associated with shallow water. An average of 84.5% (range 79-90%) of the wet weight was water. As Figure 2 shows, one would expect to find a dry weight of 290 g/m^2 in a pasture of *Cymodocea* with 100% cover at Khor Umaira in July. The corresponding wet weight would register about 1,871 g/m^2. Gessner (1971) found that leaves of turtle grass, *Thalassia testudinum*, in a dense meadow off Venezuela registered 608 g/m^2 dry weight and 2,504 g/m^2 wet weight. The mean length of the leaves was 23 cm and the water depth was 60 cm. In two sample plots of *T. testudinum* off the Florida coast, Phillips (1960) recorded dry weight values of about 325 and 98 g/m^2. The lower biomass was associated with shallower water.

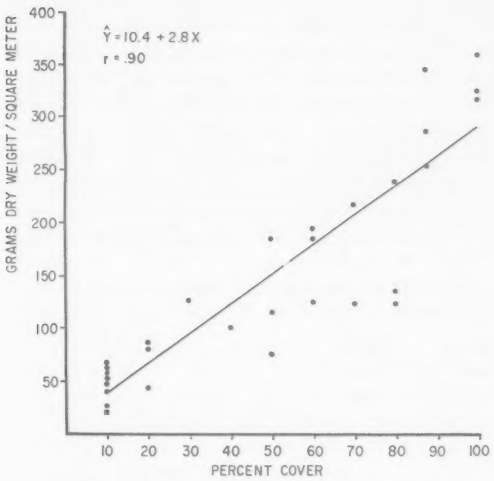

FIGURE 2.—Above-ground dry weight of *Cymodocea serrulata* regressed on field estimates of plant cover made at Khor Umaira.

The standing crop of an equally mixed pasture of *C. serrulata* and *S. isoetifolium* at Khor Umaira can be obtained from cover estimates in Figure 3. Leaf blades of both species here were less than 20 cm. On the average, water amounted to 88.7% of the wet weight of the leaves (range 83-91%).

In order to determine some chemical parameters associated with dense sea grass pasture, water samples were collected just above the leaves of an equally mixed stand of *C. serrulata* and *S. isoetifolium* with 100% cover at a depth of 1.75 m (at low tide) at 0915 h on 30 July 1972. The pH was determined using colorimetric standards and the other chemical parameters were obtained using standard methods for water analyses. The results are as follows: temperature 29.2°C; salinity 36.50‰; chlorinity 20.19‰; pH 8.2; free carbon dioxide 10 ppm; dissolved oxygen 5 ppm; total alkalinity 122 ppm, with 36 ppm as carbonate alkalinity and 86 ppm as bicarbonate alkalinity; magnesium chloride 4,000 ppm; and calcium chloride 999 ppm.

Substrate samples were taken at the same site and at the same time as the water samples. The substrate of this site consists largely of coarse fragments of shells. The bottom sample analyzed was a composite of five samples taken at a depth of 0-2.5 cm. The pH was obtained using a glass electrode, particle size was based on material passing a 2-mm sieve, and the other chemical parameters were determined using standard soil testing techniques. The results are as follows: pH 7.2; sand 97%; silt 3%; clay 0%; phosphorus 0.027 mg/g substrate; calcium 73.5 mg/g substrate.

The regression lines in Figures 2 and 3 show that given equal cover, standing crop is greater in a mixed pasture of *Cymodocea* and *Syringodium* than in a homogeneous stand of *Cymodocea*. This may be due to the close packing of the terete leaves of *Syringodium* in the mixed pasture.

The caloric content of four genera of sea grasses collected in the bay at Khor Umaira and one genus *(Thalassodendron)* collected off the nearby coast at a depth of 4.5 m, are given in Table 1. The data show that the caloric content of the five genera are very similar.

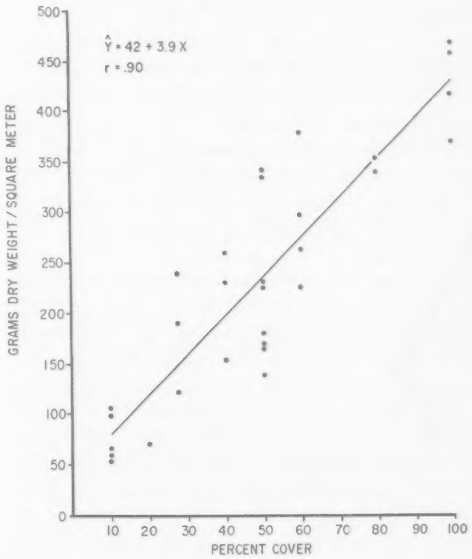

FIGURE 3.—Dry weight of a stand consisting of equal quantities of *Cymodocea serrulata* and *Syringodium isoetifolium* regressed on field estimates of plant cover. All data are from Khor Umaira and include only above-ground tissue.

For comparative purposes, the caloric content of five genera of sea grasses collected in various areas of the world and known to be eaten by green turtles there, are provided in Table 2. All of the samples from the South Pacific were burned according to the methods of Lieth (1968). It is likely that these values would be about 8% higher if independent ash determinations were made with a muffle furnace. Although green turtles were not actually seen feeding around Fulanga in the Lau Group of the Fiji Islands, leaves of *Halodule uninervis* collected in November 1970 around Fulanga registered 4.02 kcal/g dry wt, ash free when combusted by the Lieth (1968) method. *T. testudinum* around Grand Cayman Island is currently collected by a special underwater harvester and along with specially prepared food pellets is fed to captive green turtles in the turtle farm on Grand Cayman. Likewise, on some of the Tonga Islands, *Syringodium* and *Halodule* wrack washed up on the strand in large quantities after storms is fed to captive turtles kept in kraals. The findings reported in Tables 1 and 2 show that the caloric content of leaves of various kinds of sea grass are similar despite the fact the samples were collected at different times of the year and at widely scattered places. However, some interarea differences are evident in that the energy content of tissue of five genera from the Gulf of Aden (Table 1) averaged about 0.15 kcal/g dry wt, ash free, higher than the four genera from the South Pacific (Table 2) as measured by the Lieth method.

The caloric content of sea grasses reported in this paper are very similar to the value of 4.41 kcal/g dry wt, ash free reported for *Phyllospadix scouleri* by Paine and Vadas (1969). The caloric values are also similar to some of the benthic marine algae collected off the coast of the State of Washington where the modal values of green, red, and brown algae were respectively, 4.90, 4.75, and 4.45 kcal/g dry wt, ash free (Paine and Vadas, 1969). For 32 samples of aquatic monocotyledons, Cummins and Wuycheck (1971) give a mean of 4.77 kcal/g dry wt, ash free and for 359 samples of aquatic algae they list a mean of 4.63 kcal/g dry wt, ash free, but none of their samples were sea grasses.

The number of calories in the standing crop of sea grasses at Khor Umaira can be estimated by referring to the regression lines in Figures 2 and 3. For example, assuming that leaves of *C. serrulata* represent 3.01 kcal/g dry wt (Table 1) then a pasture with, say, 50% cover contains about 453 kcal/m^2 (Figure 2).

There are extensive sea grass pastures in some shallow coastal waters (for distribution see den Hartog, 1970) but before turtle ranching can become a reality, studies are needed on the energy provided by epiphytes and animal prey. It is likely that green turtles obtain some nutritional value from the epiphytic organisms on the sea grass leaves. Allen (1971) has provided detailed information on the energetics of epiphytic algae and bacteria in a lake ecosystem. Further, the digestive processes of green turtles ought to be examined in relation to the protein content of sea grasses and other food. Occasionally, it has been observed that

TABLE 1.—Caloric values of sea grasses (leaves only) at Khor Umaira. The plants were collected on 28, 29, and 30 July 1972.

Species	kcal/g dry wt	Ash %	kcal/g dry wt, ash free[1]
Halophila ovalis	3.07	33	4.58 (4.21)
Cymodocea serrulata	3.01	34	4.56 (4.19)
Halodule uninervis	3.09	32	4.54 (4.23)
Syringodium isoetifolium	3.12	33	4.66 (4.29)
Thalassodendron ciliatum	3.11	33	4.64 (4.27)

[1] Caloric values in parentheses were obtained using methods of Lieth (1968). The corresponding ash free caloric values are based on independent ash determinations; see text for explana-

TABLE 2.—Caloric values of sea grasses (leaves only).

Species	Local name	Locality	Date collected	kcal/g dry wt, ash free[1]
Halodule wrightii	Sigret	Masirah Isl., Arabian Sea	15 June 1972	4.54 (4.13)
Halophila ovalis	Sigret	Masirah Isl., Arabian Sea	15 June 1972	4.51 (4.10)
Thalassia testudinum	Turtle grass	Grand Cayman Isl., Caribbean Sea	24 May 1972	4.59 (4.24)
Halodule uninervis	Herbe à tortue	Noumea, New Caledonia	25 Nov. 1970	(4.07)
Cymodocea serrulata	Herbe à tortue	Noumea, New Caledonia	25 Nov. 1970	(4.09)
Halophila ovalis	Vutia	Suva, Fiji Isl.	10 Nov. 1970	(4.07)
Syringodium isoetifolium	Vutia	Suva, Fiji Isl.	10 Nov. 1970	(4.10)
Halodule uninervis	Limu	Nukualofa, Tonga Isl.	24 Oct. 1970	(4.07)
Syringodium isoetifolium	Limu	Nukualofa, Tonga Isl.	24 Oct. 1970	(4.11)

[1] Caloric values in parentheses were obtained using methods of Lieth (1968). The other three caloric values are based on independent ash determinations: see text for explanation.

adult green turtles have eaten invertebrates (viz. crustacea, snails, jellyfish, sponges). The importance of these animals to the nutrition of green turtles has yet to be determined. Studies on the effect of different intensities of turtle grazing on the sea grass community are also needed, especially if under high grazing pressure the entire plant is pulled up. In regards to the regrowth of sea grass, Phillips (1960) has demonstrated that *T. testudinum* off the Florida coast will regrow to normal height in about 3 mo after being cut to ground level. Taylor, Saloman and Prest (1973) have recently shown that *T. testudinum* suffered no damage when the leaves were harvested twice during a 6 mo growing season in Tampa Bay, Fla., and they postulated that in deeper or warmer waters where the growing season is protracted three or more cuttings per year may be possible.

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NOTES

FOSSIL TREE STUMPS FOUND IN SITU ON SUBMERGED RIDGE AT AMCHITKA ISLAND, ALASKA[1]

Two ancient tree stumps, in situ and partially embedded in bedrock, were found at a depth of 23 m off the Bering Sea coast of Amchitka Island in the western Aleutians. The stumps were found by the authors in October 1972 approximately 1.1 km north-northwest of Banjo Point (Figure 1) during underwater surveys of physical and biological damage associated with recent nuclear testing on Amchitka.

The two stumps were located at the base of a narrow ridge of bedrock which is over 100 m in length, rises abruptly from a generally level bedrock bottom at a depth of about 23 m, and is oriented approximately normal to the adjacent coastline. The height and thickness of the ridge range from about 4 to 8 m, and its clifflike faces are nearly vertical. This ridge is thought to be an abandoned erosional sea stack related to a brief stillstand of sea level during Pleistocene time at about 20 to 30 m below present sea level (L. M. Gard, U.S. Geological Survey, Denver, CO 80225, pers. comm.).

Each of the stumps is about 1 m high and seems to have a trunk diameter of about 30 to 40 cm. The one stump that was studied in detail is located in a slight recess at the base of the west face of the ridge (Figure 2). The base of the stump is at the level of the generally horizontal bedrock sea floor which extends westward from the ridge; at this place the ridge face is 8 m high. The stump itself is mostly surrounded by undisturbed bedrock (Figures 3, 4). With the exception of lower root extremities which extend outward several centimeters from the base of the cliff and disappear into the adjacent horizontal substrate, the stump is flush with or slightly recessed into the cliff face.

Directly above the stump in the roof of the rock recess is a vertical cylindrical hole about 20 cm in diameter and depth. The existence of a small diameter opening extending upward through the rock was indicated by a stream of fine air bubbles escaping from the cliff face about 4 m above the stump. The air was from the divers' exhalations that had become trapped in the hole above the stump. It appears that the stump had originally been totally encased in bedrock but was then partly exposed as the cliff face eroded away. The hole above the stump may once have contained a higher portion of the tree trunk, but the wood within the hole disintegrated, leaving the cavity in the rock.

Additional wood material was found in the immediate vicinity of the stump. On the horizontal bedrock sea floor within 2 to 5 m from the

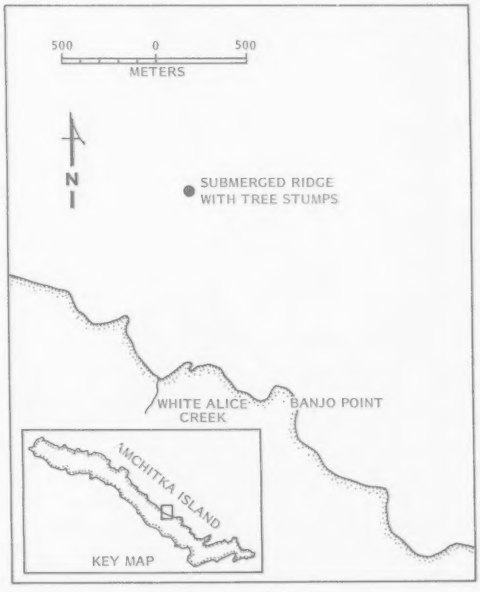

FIGURE 1.—Location of submerged ridge with in situ tree stumps in relation to the adjacent shoreline of Amchitka Island, Alaska.

[1] This work was supported by the U.S. Atomic Energy Commission as a part of its Amchitka Bioenvironmental Program.

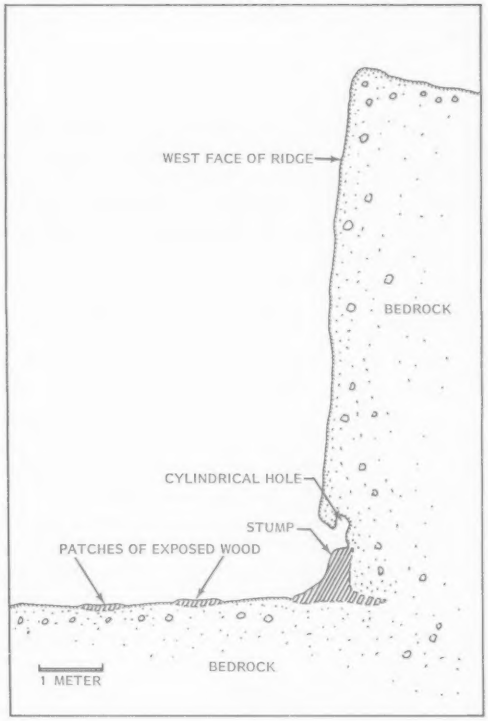

FIGURE 2.—Diagram showing approximate position of stump in relation to surrounding substrate features.

stump, several small areas of wood adhere tightly to or are partly encased in the bottom. The appearance and texture of this wood is similar to that of the stump, except that these small patches are worn down with upper surfaces flattened and generally conforming to the shape of the underlying bedrock. Although no direct connections were traced between these wood patches and the stump, their proximity and positions in relation to the stump suggest that they may be remnants of roots of the same tree. Probably buried in the substrate during the tree's life, the root remnants have now been exposed by the gradual eroding away of the rock in which they were encased.

Small samples of wood were collected from each stump. The wood is very dark brown in color and quite soft when wet but appears to be at least partially coalified. Pieces can easily be broken off or dug out with a knife. When dried, the wood becomes harder and more brittle and tends to distort and check. A sample of the wood was identified[2] as being from a coniferous tree, but further identification was not possible because the features necessary for generic identification had been removed by long-time hydrolysis.

A sample of the wood was submitted for radiocarbon dating. The indicated age of the wood exceeded 40,000 yr, the age limit of the C-14 technique of the laboratory[3] performing the analysis.

[2]Microscopic examination and identification was done by B. F. Kukachka, Center for Wood Anatomy Research, U. S. Department of Agriculture, Forest Service, Forest Products Laboratory, Madison, WI 53705.

[3]Radiocarbon dating was done by Teledyne Isotopes, Westwood, NJ 07675.

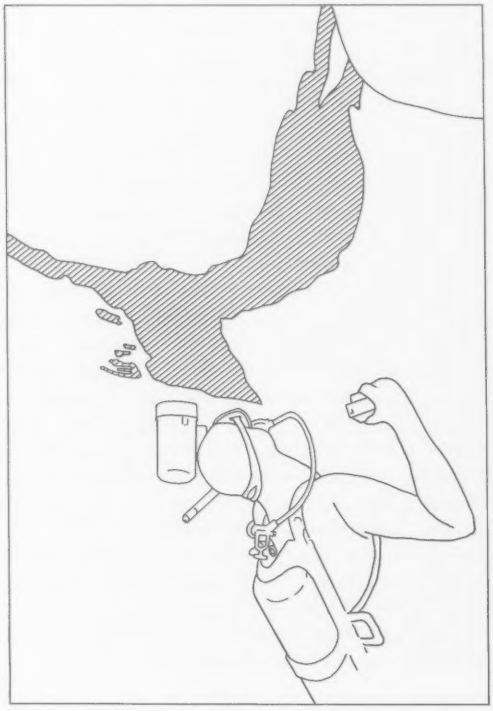

FIGURE 3.—Diagram indicating exposed wood (cross hatching) of the stump shown in the photograph of Figure 4.

FIGURE 4.—Outcrop of in situ stump at 23 m depth. Note texture of the volcanic mudflow deposit above the stump.

The exposed parts of the stumps were partially encrusted with living organisms such as coralline algae, bryozoans, and sponges, but much of the exposed wood surface was barren of organisms. There was no visible evidence of any biological degradation of the wood, that is, no borer holes or indication of decay. The surfaces of the wood appeared to be shaped principally by mechanical weathering or erosion. Unlike new wood exposed in a marine environment, the wood of the stumps appears to have been immune to the usual attacks of wood-boring organisms. During the period of total encasement in the rock substrate, the wood probably underwent chemical changes that resulted in immunity to biodegradation.

As stated earlier and as shown in Figure 4, the substrate in direct contact with the stumps was undisturbed bedrock. Rock samples we obtained from fresh rockfalls along the cliff face containing the stumps were identified as coming from volcanic breccia of the Chitka Point Formation of the Miocene age (L. M. Gard, pers. comm.). The Chitka Point Formation is composed of subaerial lava flows, breccias, tuffs, and conglomerates derived from a volcano which must have been located on western Amchitka and eastern Rat Islands (Carr et al., 1971; L. M. Gard, pers. comm.). Potassium-argon dates obtained on lavas of the upper part of the Chitka Point Formation indicated an age of at least 12.4 ± 1.1 million yr (Carr et al., 1971).

Amchitka and all of the Aleutian Islands are now devoid of naturally occurring trees. Evidence that trees once grew on Amchitka does exist, however. During Miocene time, trees and other carbonaceous material were often incorporated into volcanic mudflows and debris flows of the Chitka Point Formation, as evident by the presence of this material in many of the outcrops of breccias, tuffs, and conglomerates along the Bering coast of Amchitka (Powers, Coats, and Nelson, 1960; L. M. Gard, pers. comm.).

The significance of the tree stumps reported in this paper derives from their in situ location 23 m below present sea level. Because of the offshore and submerged location of these stumps, they represent a time when the island was not only forested but larger and at least 23 m higher in relation to sea level.

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ESTIMATION OF RATES OF TAG SHEDDING BY NORTHWEST ATLANTIC BLUEFIN TUNA[1]

A joint experiment was initiated by the Fisheries Research Board of Canada (FRBC), the National Marine Fisheries Service, and the Woods Hole Oceanographic Institution (WHOI) in 1971 under the leadership of F. Mather to estimate the rates of tag shedding by bluefin tuna. Five hundred and eighty bluefin tuna were double tagged with one of four types of dart tags off the east coast of the U.S. during the 1971 fishing season. Two types of darts, metal and plastic, were used and tags supplied by FRBC were slightly different from tags supplied by WHOI. Tags and tagging procedures

[1] Contribution No. 3010, Woods Hole Oceanographic Institution, Woods Hole, MA 02543.

TABLE 1.—Tag releases and returns from east coast of U.S. bluefin tuna double tag study.

Agency and tag type	1971 Double tag releases	1971 First year returns			1972 Second year returns		
		n_{dd1}	n_{ds1}	t_1 (days)	n_{dd2}	n_{ds2}	t_2 (days)
FRBC							
Plastic dart	140	16	1	24.4	7	8	369.8
Metal dart	128	9	1	19.4	9	11	376.0
WHOI							
Plastic dart	150	4	0	7.2	20	9	349.9
Metal dart	162	4	1	18.6	10	9	371.1
Total							
Plastic dart	290	20	1	19.8	27	17	357.3
Metal dart	290	13	2	19.1	19	20	373.7
Total	580	33	3	19.5	46	37	364.7

were those described by the Food and Agriculture Organization (1972). The 1971 releases and returns in 1971 and 1972 are shown in Table 1 by tagging agency and dart type.

The notation and methodology in this study follows Bayliff and Mobrand (1972):

$$n_{ddk} = F\tau N_D \pi \rho^2 e^{-(F + X + 2L)t_k}$$

$$n_{dsk} = F\tau N_D \pi \rho (1 - \rho e^{-L t_k}) e^{-(F + X + L)t_k}$$

where:

t_k = time at the middle of the kth period of length τ (k = 1, 2),

n_{ddk} = number of returns of double-tagged fish retaining both tags during the period centered at t_k,

n_{dsk} = number of returns of double-tagged fish retaining only one tag during the period entered at t_k,

N_D = number of fish released with double tags,

π = portion of tagged fish which remain alive after the Type-I (immediate) mortality has taken place,

ρ = portion of the tags which are retained after Type-I (immediate) shedding has taken place,

F = instantaneous rate of fishing mortality,

X = instantaneous rate of other mortality (other includes natural mortality, Type-II (long-term) tagging mortality and apparent mortality caused by migration from the fishery), and

L = instantaneous rate of shedding of tags.

Bayliff and Mobrand showed that

$$\ln \frac{2n_{ddk}}{n_{dsk} + 2n_{ddk}} = -Lt_k + \ln\rho = Y_k$$

where Y_k is an estimate of the log of the proportion of tags retained up to time t_k.

Estimates of Y_k are shown in Table 2. Estimates of L and ρ are shown in Table 3. Although some differences among categories are indicated, a chi square test for differences in returns among categories was not significant at the 90% level of confidence. Thus the differences do not appear to be large enough to rule out the use of

TABLE 2.—Intermediate results in estimates of shedding rates from 1971 U.S. east coast bluefin double tag study.

Agency and tag type	Y_1	Y_2
FRBC		
Plastic dart	-0.03077	-0.45199
Metal dart	-0.05407	-0.47692
WHOI		
Plastic dart	0	-0.20294
Metal dart	-0.11778	-0.37156
Total		
Plastic dart	-0.02469	-0.27370
Metal dart	-0.07411	-0.42286
Total	-0.04445	-0.33802

TABLE 3.—Estimates of ρ and L from 1971 U.S. east coast bluefin double tagging study.

Agency and tag type	$\ln\rho$	L on daily basis	ρ	L (on annual basis)
FRBC				
Plastic dart	-0.00102	0.0012195	0.999	0.44512
Metal dart	-0.03106	0.0011858	0.969	0.43282
WHOI				
Plastic dart	0.00426	0.0005922	1.004	0.21615
Metal dart	-0.10439	0.0007199	0.901	0.26278
Total				
Plastic dart	-0.01008	0.0007378	0.990	0.26929
Metal dart	-0.05532	0.0009835	0.946	0.35898
Total	-0.02787	0.0008504	0.973	0.31041

the estimates obtained from the combined data. These estimates of $\rho = 0.973$ and $L = 0.31041$ are close to the estimates of Bayliff and Mobrand (1972) of $\rho = 0.913$ and $L = 0.278$ for yellowfin tuna in the eastern Pacific.

Acknowledgments

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DISTRIBUTION AND ABUNDANCE OF THE SAND DOLLAR, *DENDRASTER EXCENTRICUS*, OFF THE COAST OF OREGON AND WASHINGTON

Dendraster excentricus is one of two known species of Clypeasteroid echinoids occurring along the Pacific coast of North America from British Columbia southward to Mexico. It lives on sandy bottoms from the low water zone to a depth of about 90 m[1] (Raup, 1956). Large beds of these animals have been reported in southern Puget Sound, Monterey Bay, Newport Bay, San Diego Bay, and El Estero de Punta Banda — just south of Ensenada, Mexico (Ricketts and Calvin, 1952). Merrill and Hobson (1970) made detailed observations on the behavior, distribution, and biotic relationships of *D. excentricus* along the Pacific coast of California and Baja California, Mexico. They remarked that relatively little was known about the populations of sand dollars along the exposed outer

[1] Richard J. Merrill, Department of Biological Sciences, University of California, believes this is too deep for *D. excentricus* and may refer to *D. laevis* (pers. comm.).

coast northward from Point Conception, Calif. The report presents new information on the distribution and abundance of sand dollars along the coast of Oregon and Washington.

Materials and Methods

The Seattle-based research vessel *John N. Cobb* of the National Marine Fisheries Service took large numbers of *D. excentricus* while dredging during two clam surveys along the Washington and Oregon coast in the summer of 1969. The dredge used during the surveys was an east coast type hydraulic clam dredge (Figure 1) which weighed approximately 1,021 kg (2,250 lb) and had a blade 91.4 cm (36 inches) wide with a maximum digging depth of 35.6 cm (14 inches). Each dredge haul was of 10 min duration, made from north to south, and covered an average distance of 0.56 km (0.3 nautical mile). The bottom area "swept" by each haul was approximately 508 m^2 (5,472 ft^2). Hauls were made only on sandy bottom areas believed to be free of rocks.

The first survey was conducted in June along the Washington coast between Cape Flattery and the Columbia River. Forty-six hauls were made: 9 at 9-11 m, 15 at 13-15 m, 8 at 16-18 m,

FIGURE 1.—A modified east coast type hydraulic clam dredge with a catch of over 1,000 lb of sand dollars being lifted board the RV *John N. Cobb*.

TABLE 1.—Average sand dollar catches off the Washington coast in kilograms per 10-min dredge haul and density (number of sand dollars) per square meter of bottom area. The catches are the total catch at each station, divided by the number of hauls shown in parentheses.

Sampling area (Lat)[1]	Catch, by sampling depth									
	9-11 m		13-15 m		16-18 m		24-27 m		29-37 m	
	Avg. catch (kg)	Avg. density (no./m²)	Avg. catch (kg)	Avg. density (no./m²)	Avg. catch (kg)	Avg. density (no./m²)	Avg. catch (kg)	Avg. density (no./m²)	Avg. catch (kg)	Avg. density (no./m²)
46°23.0′N	—[2]	—	0 (6)	0.0	0 (2)	0.0	—	—	—	—
46°34.5′N	408 (3)	26.7	11 (1)	0.7	0 (1)	0.0	—	—	—	—
46°51.0′N	—	—	95 (2)	6.2	—	—	—	—	—	—
47°00.0′N	121 (1)	7.9	—	—	0 (1)	0.0	0 (1)	0.0	0 (1)	0.0
47°05.0′N	378 (2)	24.8	404 (3)	26.4	<1 (1)	0.0	—	—	—	—
47°34.0′N	<1 (3)	0.0	0 (3)	0.0	0 (3)	0.0	—	—	—	—
47°45.0′N	—	—	—	—	—	—	0 (5)	0.0	—	—
48°15.5′N	—	—	—	—	—	—	—	—	0 (7)	0.0
Total averages	234 (9)	15.3	94 (15)	6.2	<1 (8)	0.0	0 (6)	0.0	0 (8)	0.0

[1]Approximate midpoint of hauls.
[2]Dashes (—) indicate that no haul was made at the station.

TABLE 2.—Sand dollar catches off the Oregon coast in kilograms per 10-min dredge haul and density (number of sand dollars) per square meter, September 1969.

Sampling area		Catch, by sampling depth									
		9 m		14 m		18 m		23 m		27 m	
Lattitude[1]	Coastal landmark	Catch (kg)	Density (no./m^2)	Catch (kg)	Density (no./m^2)	Catch (kg)	Density (no./m^2)	Catch (kg)	Density (no./m^2)	Catch (kg)	Density (no./m^2)
43°25.7′N	Coos Bay	1,814[3,4]	118.9	603	39.6	363	23.8	0	0.0	0	0.0
43°27.3′N	—	0	0.0	0	0.0	499	32.7	0	0.0	0	0.0
43°31.1′N	—	—[2]	—	0	0.0	0	0.0	0	0.0	0	0.0
43°34.9′N	Ten Mile Cr.	102[3]	6.7	454[3]	29.8	454	29.8	907	59.4	0	0.0
43°37.9′N	—	0	0.0	91	5.9	0	0.0	1,179	77.3	680	44.6
43°42.9′N	Umpqua River	1,134[3]	74.3	1,270	83.2	14	0.9	4	0.3	0	0.0
43°47.0′N	Tahkenitch C.	113[3,4]	7.4	1	0.1	0	0.0	544	35.7	499	37.2
43°51.0′N	Siltcoos R.	567[3]	37.2	45	3.0	567	37.2	23	1.5	23	1.5
43°55.0′N	—	0	0.0	2	0.1	0	0.0	0	0.0	0	0.0
43°59.1′N	Siuslaw R.	1[3]	0.1	0	0.0	0	0.0	0	0.0	0	0.0
44°03.1′N	Sutton Cr.	1,134[3,4]	74.3	0	0.0	0	0.0	0	0.0	0	0.0
44°07.3′N	Hecata Hd.	—	—	—	—	0	0.0	0	0.0	0	0.0
44°11.3′N	Rocky Knoll	23[3]	1.5	<1	0.0	0	0.0	0	0.0	0	0.0
44°15.4′N	Gwynn Knoll	113[3,4]	7.4	2[3]	0.1	0	0.0	0	0.0	0	0.0
44°19.4′N	Yachats R.	363[3,4]	23.8	0	0.0	<1	0.0	<1	0.0	0	0.0
44°23.7′N	Alsea Bay	4[3]	0.3	2	0.1	1	0.1	0	0.0	0	0.0
44°27.7′N	Seal Rocks	—	—	0	0.0	—	—	0	0.0	0	0.0
Total averages		384	25.1	154	10.1	118	7.8	156	10.2	71	4.9

[1] Approximate midpoint of hauls.
[2] Dashes (—) indicate that no haul was made at the station.
[3] Live specimens, all others were dead (empty tests).
[4] Catches which were sampled for width measurements.

6 at 24-27 m, and 8 at 29-37 m. The second survey was conducted in September between Coos Bay and Newport, Oreg. Eighty hauls were made: 14 at 9 m, 16 at 14 m, 16 at 18 m, 17 at 23 m, and 17 at 27 m. The areas sampled were uniformly spaced along the coast, approximately 7.4 km (4 nautical miles) apart.

Sand dollar catches were weighed using a dynamometer on the first several hauls of each of the surveys. Weights of catches were estimated on the remaining hauls according to the portion of the cod end and dredge that was filled. During the Washington survey, which was largely involved with development of dredging techniques, no data were collected on the proportion of live and dead specimens. On the Oregon survey the incidence of live specimens and "empty tests" (dead specimens) in each haul was recorded. Also width measurements were made on five samples of live specimens taken at a depth of 9 m. Sample sizes varied from 136 to 310 individuals.

Results

Washington. — Nearly all the *D. excentricus* were taken in the two shallowest depth intervals — 9-10 and 13-15 m (Table 1). No sand dollars occurred in hauls made at depths greater than 18 m. The largest single catch, 1,209 kg (2,666 lb), occurred in a depth of 15 m off Ocean City (lat. 47°05.0′N), and catches of up to 454 kg (1,000 lb) were taken in 9-11 m just south of the Willapa Bay entrance (lat. 46°34.5′N). The average density in each of the above two sampling areas was over 26 sand dollars per m^2.[2]

Oregon. — There was a consistent pattern in the incidence of live and dead (empty test) sand dollars with increasing depth in Oregon waters — only live animals were taken in the shallower water and only dead animals were taken in the deeper water (Table 2). The largest catch

[2]All estimates of numbers of sand dollars from weight of specimens based on an average weight per specimen of 30 gm (15.1 specimens per lb).

(1,814 kg, or an estimated 60,400 specimens) was at 9 m and occurred near Coos Bay. The 14-m depth was an area of transition between living and dead sand dollars. Catches made at 18, 23, and 27 m were composed entirely of dead animals. At these depths, the largest catches along the coast occurred between Ten Mile Creek and Siltcoos River.

Mean widths of the five samples of live specimens ranged from 76.4 to 85.9 mm; the overall mean was 80.1 mm. The catches from which these samples were taken are marked with a footnote in Table 2.

Discussion

Merrill and Hobson (1970) reported that two types of distribution patterns occur in sand dollar populations along the protected outer coast. In one type, the populations run parallel to shore as dense bands and maintain a characteristic pattern that is reformed when disrupted by occasional heavy seas. The outer margin of these populations is well-defined in 4-12 m of water and here the largest individuals and greatest densities occur. The other type of distribution is similar, except that it extends into deeper water, below about 10-15 m; individuals become progressively smaller with depth.

These distribution patterns are apparently similar off the exposed outer coasts of Oregon and Washington. My findings off Oregon and Washington indicate well-defined seaward limits, as essentially no live *D. excentricus* were taken by the dredge at depths below 15 m.

McCauley and Carey (1967) collected *D. excentricus* off Oregon in depths of 8 to 56 m. They found the mean widths of specimens to be 78.2 mm at 8 to 13m, 35.8 mm at 22 m, and less than 10 mm at 50 m. They concluded that mean widths show a decrease in size with depth, suggesting that animals may move shoreward with increase in size or that in some way depth may influence growth. They apparently sampled both the near-shore and deeper water types of distribution patterns.

Merrill and Hobson (1970) speculated that available food for *D. excentricus* off the protected outer coast is most abundant just seaward of the breaker line, where the water is about 10 m deep, and that beyond this depth available food decreases with depth. Our dredge catches of the species off Oregon and Washington support the hypothesis that optimum conditions for *D. excentricus* exist inside the 15-m depth interval.

It is difficult to explain why large numbers of dead sand dollars were found primarily in the deeper depths sampled during our surveys (18-27 m). Merrill and Hobson (1970) found that at Zuma Beach, Calif. (a protected outer coast area) much of the sand dollar population in shallow water is swept or carried seaward during heavy seas, but when the sea is calm individuals in the seaward part of the colony move shoreward. This seaward movement during heavy seas may be even more extensive in populations in exposed outer coast areas off Oregon and Washington where storms are often more frequent and severe. Empty tests would be even more subject to wave action and currents than live specimens. During heavy seas they may be swept seaward where they accumulate.

My findings support earlier observations that *D. excentricus* is widely distributed and, in addition, is abundant in many sandy bottom areas within a depth of 15 m off the coast of Oregon and Washington.

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